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SOME PRELIMINARY OBSERVATIONS BEARING ON THE NUTRITION OF *LIMNORIA*^{1,2}

R. D. SCHAFER³

Immaculate Heart College

AND

CHARLES E. LANE

The Marine Laboratory, University of Miami

ABSTRACT

Limnoria of both sexes and all ages did not survive when they were allowed to feed only on sterile wood in sterile sea water. No fecal pellets were produced under the conditions of this experiment. When *Limnoria* were given living mycelium of the fungus *Peritrichophora integra* as the sole food source the mortality rate approached the normal. Amino acid analyses of *Limnoria*, of sterile wood in which it may live, and of the fungi which normally infects the wood suggest that the fungus makes a greater contribution to the nutrition of this borer than has been heretofore suspected.

INTRODUCTION

Marine wood-boring animals generally appear to be capable of effecting enzymatic hydrolysis of the wood in which they live. Ray and Julian (1952) showed that *Limnoria* possesses an active enzyme complex for the hydrolysis of cellulose and some other components of wood. Harrington (1922), Boynton and Miller (1927) and Greenfield and Lane (1953) have demonstrated that *Teredo* also contains an active cellulase enzyme complex. Mature wood has been reported by Wise (1946) to contain only 0.3 per cent total nitrogen. This small total concentration is made up of a relatively small number of amino acids, probably associated as simple proteins and short chain polypeptides. Lasker and Lane (1953) and Drisko and Hochman (1957) have presented evidence to suggest that wood alone is not an adequate protein source for *Teredo*. The former authors suggest that the wood is probably supplemented by planktonic organisms which are introduced into the animal in the respiratory current of water pumped

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through the mantle cavity. *Limnoria* lacks both the mechanism and the opportunity to filter planktonic organisms from the surrounding water. It is the purpose of the present communication to present preliminary observations and experiments which seek to clarify the nitrogen nutrition of *Limnoria tripunctata*, the most abundant of the local species.

MATERIALS AND METHODS

Meyers and Reynolds (1957) have emphasized that wood exposed in the sea is rapidly and universally attacked by various species of marine fungi. It has been suggested by Isham and Tierney (1953) that wood must be "conditioned" by suitable soaking and the development of a microflora and fauna before it may be successfully invaded by larval teredine borers. It was thought that *Limnoria* might have a similar nutritive dependence on fungal inhabitants of wood. To investigate this possibility sterile, fungus-free wood; fungus cultured on artificial sea water medium with asparagine as the sole source of nitrogen; a naturally occurring population of *Limnoria*, and a group of *Limnoria* from which the gut and midgut diverticulae had been removed, were hydrolyzed separately in 6 N HCl. After removal of the HCl by repeated distillation *in vacuo*, the hydrolysates were spotted on Whatman #1 filter paper and chromatographed to reveal their qualitative amino acid content.

Chromatographic analysis was carried out two-dimensionally on 11 x 13½ sheets of Whatman #1 paper. N-butanol, acetic acid and water (4:1:5) was used as the first solvent and water-saturated phenol was the second solvent. The method was essentially that of Jones and Blinks (1957) with only minor modifications. Spotted papers were placed in the solvent-saturated atmosphere of the chromatographic cabinets and permitted to equilibrate. Additional solvent was added and the chromatograms were run in the ascending direction for approximately 12 hours. The papers were then dried completely in air, rotated through 90° and run in the second direction with the second solvent. Color development was achieved by dipping the dried chromatograms in 2 per cent (w/v) ninhydrin in anhydrous acetone. Solutions of known amino acids were chromatographed under the same conditions to provide standards for identification of the unknowns. No quantitative analyses were made. The completed, dried chromatograms were transilluminated on an X-ray viewer and copied photographically.

To evaluate the effect of a diet of fungus-free wood on the chromatographic pattern of *Limnoria* an attempt was made to rear a population which had fed exclusively on sterile wood. To this end twelve females with advanced embryos in the brood pouch were isolated and the young were taken as they emerged. The resulting forty-two young *Limnoria* were placed in twelve sterile flasks (litter-mates were kept together), one-fourth filled with sterile sea water and con-

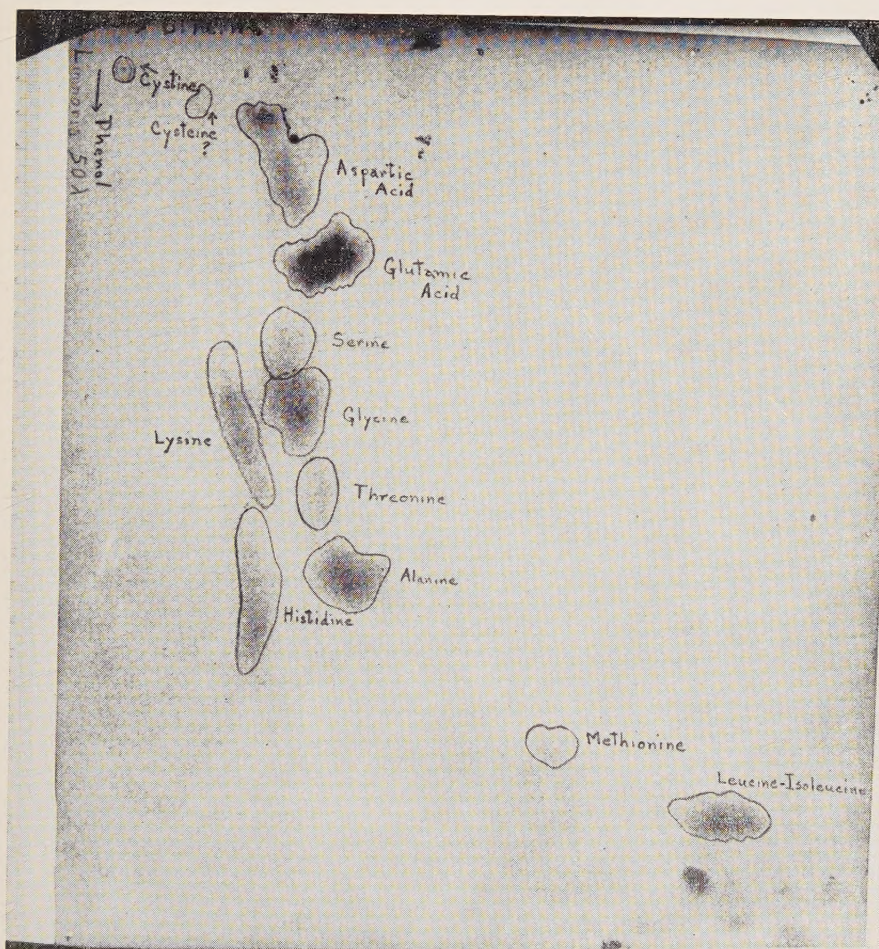


FIGURE 1. Photograph of completed two-dimensional chromatogram of acid-hydrolyzed *Limnoria*. The chromatogram of gut-free animals is identical with this one.

taining a section of sterile southern yellow pine sapwood, 5.5x3x0.4 cm.

To study the nutritional adequacy of sterile wood in sterile water, a further series of fifty gravid females was selected. These were placed in water which had been sterilized either by ultrafiltration or by autoclave. The wood was sterilized in the autoclave.

To assess the significance of fungi which are normally present in



FIGURE 2. Photograph of completed two dimensional chromatogram of acid-hydrolyzed *Lulworthia floridana*. For cultural details and for details of chromatographic manipulation see the text.

wood immersed for any appreciable length of time in sea water, and which were being denied the *Limnoria* in the previous experiments, a series of feeding experiments was performed. Autoclaved sea water and autoclaved wood were combined in sterile test tubes together with a single *Limnoria*. This was done to verify the results obtained in the earlier efforts to rear a population which had fed only on sterile wood, and to eliminate the possibility that selection had influenced the mor-

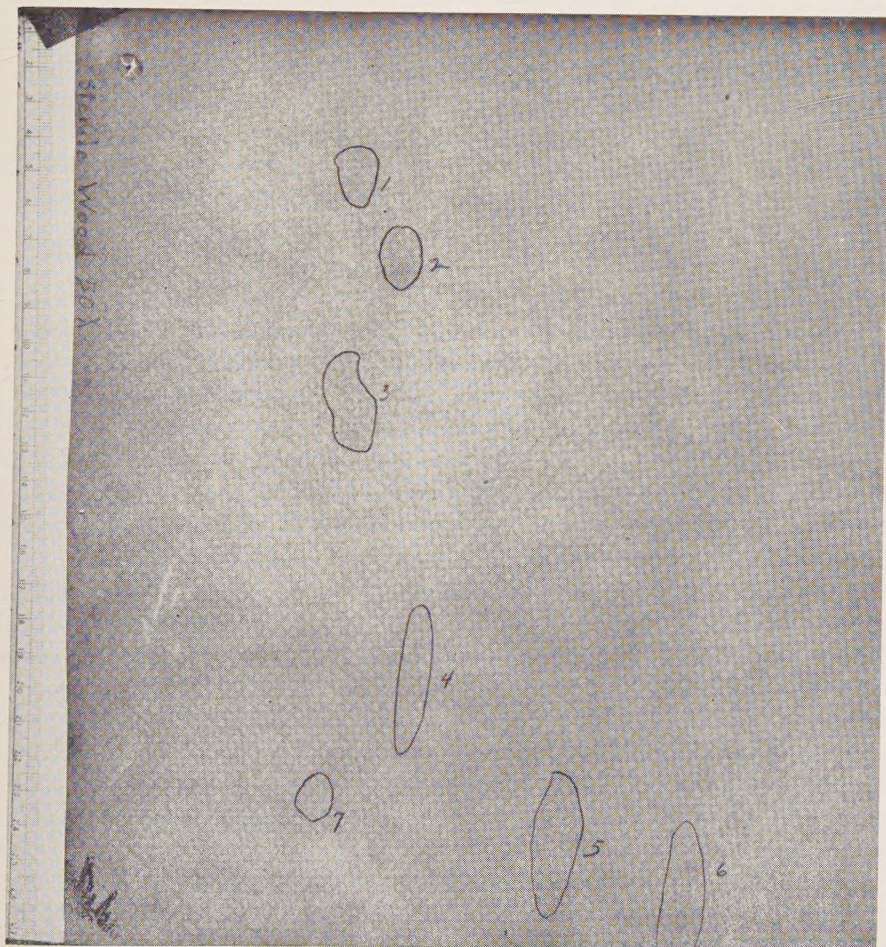


FIGURE 3. Chromatogram, prepared and photographed as were the previous figures, of sterile southern yellow pine sapwood hydrolyzed in 6 N HCl. #1 aspartic acid, 2 glutamic acid, 3 glycine, 4 alanine, 5 methionine, 6 leucine-isoleucine complex and 7 histidine.

tality rate. Nineteen animals were used in this experiment.

Filtered sea water and autoclaved wood were combined in fifty tubes. This combination was selected to eliminate the autoclaved sea water as a contributing factor in the high mortality. Fifty animals, selected at random, were placed on the wood each in a separate tube.

Autoclaved sea water and fragments of the living mycelial mat of the fungus *Peritrichophora integra* were combined in fifty test tubes to determine the value of the fungus for the survival of *Limnoria*. One animal was placed in each tube.

Filtered sea water and living fungus were likewise combined in fifty test tubes and to each was added a single specimen of *Limnoria*. These feeding experiments were controlled by adding pieces of wood, on which *Limnoria* had been living in the bay, to test tubes containing autoclaved sea water. One animal was likewise placed in each container.

RESULTS

The maximum survival time of animals given sterile wood in sterile water was four days. During this time no fecal pellets were produced. It should be mentioned that these experiments were conducted during a period when the laboratory temperature frequently rose to 34°C. Prolonged survival of starved *Limnoria* has only been reported for cold-water species. Control populations maintained in non-sterile wood under the same conditions of temperature, circulation and ventilation, survived and fed normally.

Of the animals placed on fungus in sterile water, 54 per cent were alive after eleven days. All of the mortality occurred in animals which left the water and climbed up the side of the tube. This behavior is attributed to low oxygen tension in the water resulting from the combined respiration of the surviving mycelial mat and of the *Limnoria*. All the animals placed on the fungus fed vigorously, some to the extent that the food supply was entirely converted to fecal pellets. Those animals kept on fungus-infected wood in autoclaved sea water survived with only two exceptions.

There were no differences in the amino acid spectrum revealed by the chromatograms of intact *Limnoria* and of those from which the digestive tract and appended diverticulae had been removed. Thirteen amino acids were identified (Figure 1).

The fungus *Lulworthia floridana*, found on wood infected with *Limnoria*, cultured in artificial sea water with asparagine as the sole source

of nitrogen, when hydrolyzed and chromatographed revealed an amino acid spectrum identical with that of *Limnoria* (Figure 2).

Sterile southern yellow pine sapwood, when hydrolyzed and subjected to chromatographic analysis, revealed the presence of only seven amino acids, as is shown in Figure 3.

DISCUSSION

When the failure of *Limnoria* to survive, or even to feed, upon sterile wood under the conditions of these experiments, is contrasted with vigorous feeding and good survival when they are fed a fungus normally found in wood exposed to a marine environment, an important nutritive role for the fungus is suggested. The exact duplication of the *Limnoria* spectrum of amino acids by the fungus *L. floridana* is not necessarily significant. Exact qualitative similarity of amino acid composition among organisms certainly does not of itself indicate nutritive dependence nor even relationship. However, when it is recalled that the only nitrogen containing materials available to *Limnoria*, apart from dissolved organic substances in sea water, are wood and its associated flora and fauna, and when it is shown that wood alone is inadequate as a source of protein nitrogen, then this biochemical resemblance between organism and known food material suggests a casual relationship.

It was not entirely unexpected to find that chromatograms of intact *Limnoria* were identical with the fungus on which they had been feeding. The digestive tracts were gorged with food materials. However, when the similarity persisted in hydrolyses of gut-free *Limnoria* then it appeared likely that amino acids of fungal origin had actually been incorporated into *Limnoria* protein.

It appears that both wood and its associated flora and fauna in nature may contribute to the nutrition of *Limnoria*. Indeed, as Meyers and Reynolds (loc. cit.) have suggested, the widely distributed marine wood-destroying fungi may prove to occupy an exceedingly important position in the marine biosphere.

SUMMARY AND CONCLUSIONS

Limnoria tripunctata of all ages and both sexes failed to survive longer than four days when they were given sterile wood in sterile water. Survival figures approached normal when *Limnoria* were given living mycelium of the fungus *Peritrichophora integra* as a sole food source, in sterile water. Amino acid analysis of *Limnoria*, of sterile

wood in which it may live, and of the fungus which normally inhabits the wood, suggests that the fungus makes a greater contribution to the total nutrition of this form than has been heretofore suspected.

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PLANKTON OF THE FLORIDA CURRENT IV. FACTORS INFLUENCING THE VERTICAL DISTRIBUTION OF SOME COMMON COPEPODS¹

H. B. MOORE AND D. L. O'BERRY
The Marine Laboratory, University of Miami

ABSTRACT

The diurnal migration of sixteen species of copepods was studied at eleven 24-hour stations in the Florida Current off Miami. The extent and direction of their diurnal migration was shown to be related to their day level. In the daytime a deep-living species was more vertically dispersed, and was found at a wider range of temperature and light conditions than a shallow-living species. Night levels were controlled largely by temperature, but the light effect was sufficient to cause all species to be more abundant at the surface on moonlit than on dark nights. In Bermuda, and at the 10-15 mile station, where all species occur at relatively shallow depths, the strength of this moonlight effect is greater for deeper-living than for shallow-living species. At the 40-mile station, where all species characteristically live deeper, the moonlight effect is greater for the shallow-living than for the deep-living species. The significance of temperature in the control of night levels is discussed in connection with geographical distribution. A diurnal rhythm in the effects of the temperature and light stimuli is suggested by the date.

INTRODUCTION

The control of the vertical distribution and diurnal migration of zooplankton is complex. We know that at least three environmental factors, temperature, light and pressure, are important in such control in the open ocean (Moore and Corwin, 1956). In coastal waters other factors such as salinity may also play a part. The depth at which zooplankton live can be accounted for to a large extent in the terms of a balance between reactions to stimuli from these three factors, each tending to produce an upward or downward movement in the animals. Under the various conditions in which the animals are found, it is possible to calculate the relative strength of the responses to these three stimuli which satisfy a condition of equilibrium. The individuals of a species do not all occur at the same level; the population exhibits a considerable vertical spread. This is too great to result from random diffusion and may be taken to imply a variation in the strength of individual responses to the stimuli of temperature, light and pressure. Analysis of equilibrium equations shows this to be true. Expressed as relative responses to unit changes of temperature and light, the upper members of a population were found to be more responsive to light

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and the lower members to temperature (Moore *et al.*, 1953; Moore and Corwin, 1956; Moore, 1955). Superimposed on this variation within the population, there was also found to be a diurnal rhythm in the relative strength of responses. Thus, the observed vertical distribution of a species on a given occasion is the resultant of three environmental conditions, one of which varies diurnally, of individual differences in response to external stimuli, and of a diurnal rhythm in the strength of this response.

Most of the work that has led to the above conclusion has been based on the study either of single species or else of groups of related species such as copepods or siphonophores. It was clear that, when whole groups such as copepods, pteropods, siphonophores or chaetognaths are compared, the same general principles of vertical control apply. The fact that different species characteristically occupy different levels and carry out different diurnal migration patterns implies specific differences in their responses to external conditions. A few generalizations with regard to specific differences were made during the study of plankton in the Bermuda area (Moore, 1949), and these are extended in the present study.

Grouping together species from all phyla studied, it was found that those species which lived deepest in the daytime performed the most extensive diurnal migration; it was typically directed upwards at night and downwards in the daytime. Species living at intermediate depths performed a similar, but less extensive, migration. Shallower species showed no diurnal migration or even a reversed type, the animals moving up in the daytime and down at night. Further, those species which lived deepest in the daytime, showed a greater extent of vertical diffuseness in the daytime than the shallow-living species. Finally, most species showed a greater abundance at the surface at night at full moon than at new moon. This correlation with moonlight was also more pronounced in the species living deeper in the daytime than in the shallower-living species.

A grant from the National Geographic Society initiated study of the plankton of the Florida Current, and the copepods from this study were reported on by Jones (1952). Later, a grant from the National Science Foundation permitted the working of a series of 24-hour diurnal migration stations, the copepods from which were studied by the junior author. The full analyses of the latter data are not completed, but they permit certain generalizations at the present stage.

MATERIAL AND METHODS

Eleven 24-hour stations were worked at intervals across the Florida Current approximately east from Miami. Two or three nets were towed simultaneously, the flight being made at successive depths which were repeated at about three to four hour intervals. This yielded thirty to forty net hauls per station, the number varying with the weather conditions. The methods used were reported by Miller *et al.* (1953). All hauls were accompanied by measurements of depth, distance towed, temperature and illumination, the latter expressed as the exponent to the base ten, on a scale on which full sunlight is + 2. All counts were reduced to the equivalent of a standard tow of one mile.

About twenty species of copepods were initially counted, but this was later reduced to sixteen species which proved to be present consistently in adequate numbers throughout the year. These are shown in Table 1.

TABLE 1
LIST OF COPEPOD SPECIES

Calanoida	
<i>Calanus minor</i> (Claus)	<i>Pleuromamma gracilis</i> Lubbock
<i>Undinula vulgaris</i> (Dana)	<i>P. abdominalis</i> Lubbock
<i>Rhincalanus cornutus</i> Dana	<i>P. xiphius</i> Giesbr.
<i>Euchaeta marina</i> Prestandrea	<i>Calocalanus pavo</i> Dana
<i>E. spinosa</i> Giesbr.	<i>Eucalanus attenuatus</i> (Dana)
Harpacticoida	
<i>Macrosetella gracilis</i> Dana	
Cyclopoida	
<i>Oithona spirostris</i> Claus	<i>Corycaeus elongatus</i> Giesbr.
<i>O. plumifera</i> Baird	<i>C. furcifer</i> Claus
<i>Corycella carinata</i> Giesbr.	

VERTICAL DISTRIBUTION AND DIURNAL MIGRATION

The best general picture of the characteristic vertical distribution of the different species is obtained by grouping together all the data from the seven stations occupied at approximately 40 miles east of Miami. Temperature conditions there are relatively constant except for seasonal changes in the surface waters. Daytime illumination also is fairly constant at any given depth, but the night values, of course, vary widely according to the phase of the moon. Data were grouped together over four hour periods, and in 100 metre depth steps, and the results are shown in Figs. 1-4.

The species fall into four groups. Five species are more abundant at the surface in the middle of the day than they are deeper down.

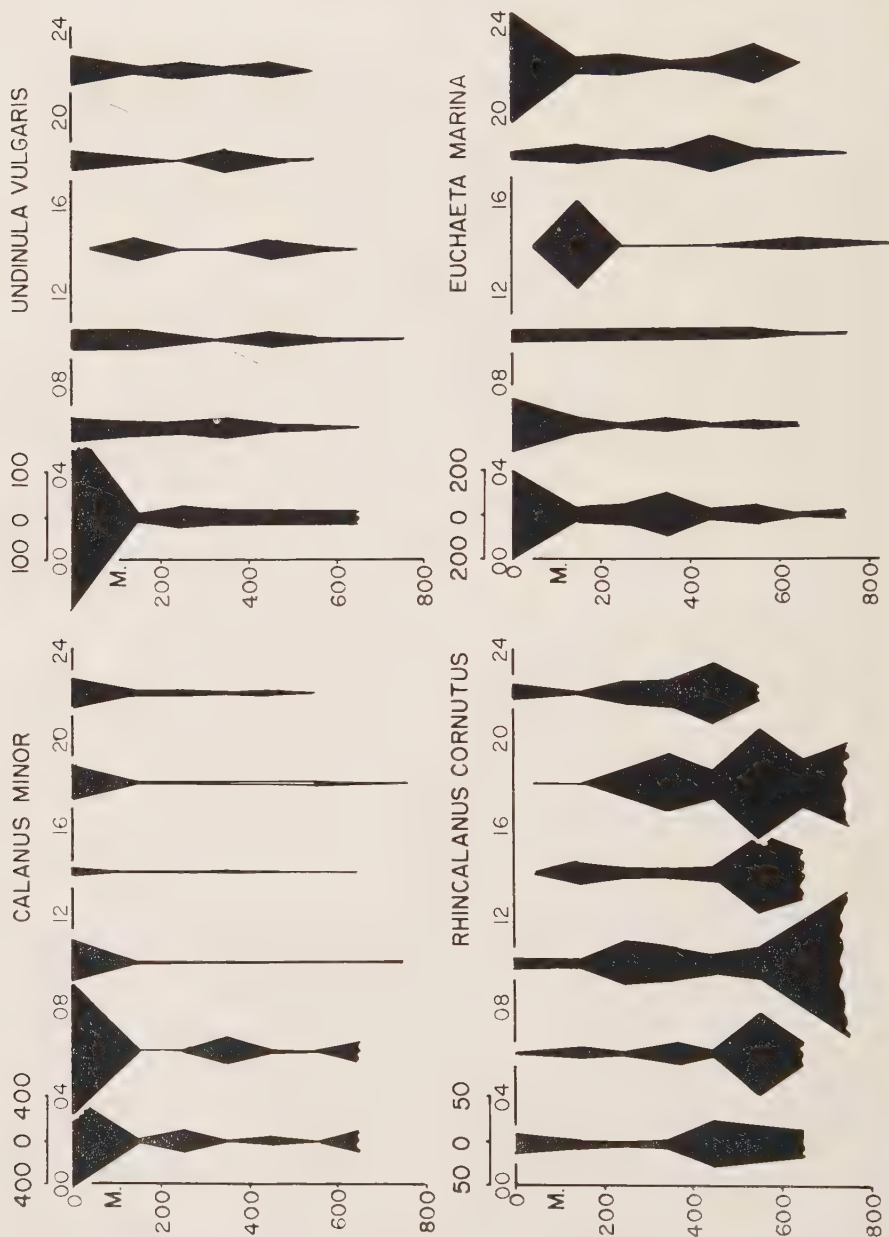


FIG. 1. Mean vertical distribution for the various species at the 40 mile station.

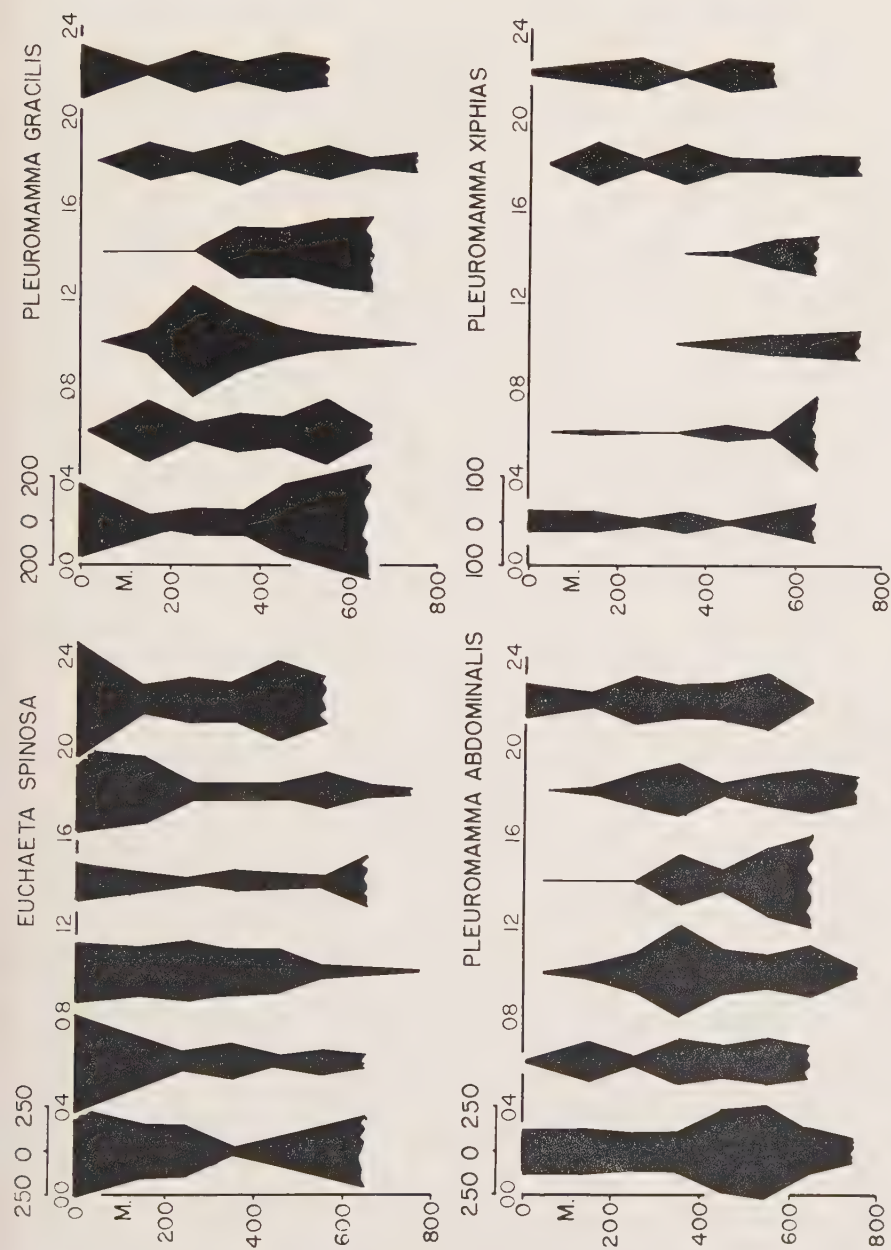


FIG. 2. Mean vertical distribution for the various species at the 40 mile station.

These are *Calocalanus pavo*, *Corycaeus furcifer*, *C. elongatus*, *Calanus minor*, and *Euchaeta spinosa*. In some there is reverse diurnal migration, the population as a whole moving upwards in the daytime; in those where there is typical diurnal migration, it is of small extent. In the second group there is a definite movement away from the surface in the daytime and a moderately extensive diurnal migration: this includes *Oithona spirostris*, *O. plumifera*, *Euchaeta marina*, *Eucalanus attenuatus* and *Undinula vulgaris*. All are deeper-living in the daytime than the first group. A third group is needed for the only Harpacticoid copepod studied, *Macrosetella gracilis*. This is a deep-living form with a very small diurnal migration, and the fact that it does not fit into the general scheme is perhaps not surprising since the Harpacticoids are aberrant in other respects. The fourth group comprises deep forms, all with a very extensive diurnal migration, and includes *Rhincalanus cornutus*, *Pleuromamma gracilis*, *P. abdominalis* and *P. xiphias*. The last of these has an average diurnal migration at the 40 mile station of over 250 metres.

RELATION OF DIURNAL MIGRATION TO DAY LEVEL

Because of the use of successive flights of nets, hauls were not available at exactly midday and midnight, so counts for these times were obtained by interpolation between those at the closest available times. Because differences in behavior had previously been found between the shallower and deeper members of the population of a given species it was necessary to designate the part of the population under consideration. This was expressed as a percentage level: thus the 30% level is that above which 30% of the population occurs. This point in the population may be traced through its diurnal changes in depth and compared with any other percentage level. It is not yet known whether particular individuals remain at the same percentage level in the population or not. The method of calculating percentage levels has already been described (Moore, 1953). Typically, the vertical distribution of a species is not symmetrical about a mean depth. The species, unless restricted by the surface or the bottom, extends further below the mode than above it, and the maximum concentration is at about the 30% level. In earlier work (Moore, 1949, etc.), species have been compared in terms of their 50% levels, but we feel that the 30% level is characteristic of a greater part of the population and it is accordingly used except where comparison with earlier work is called for.

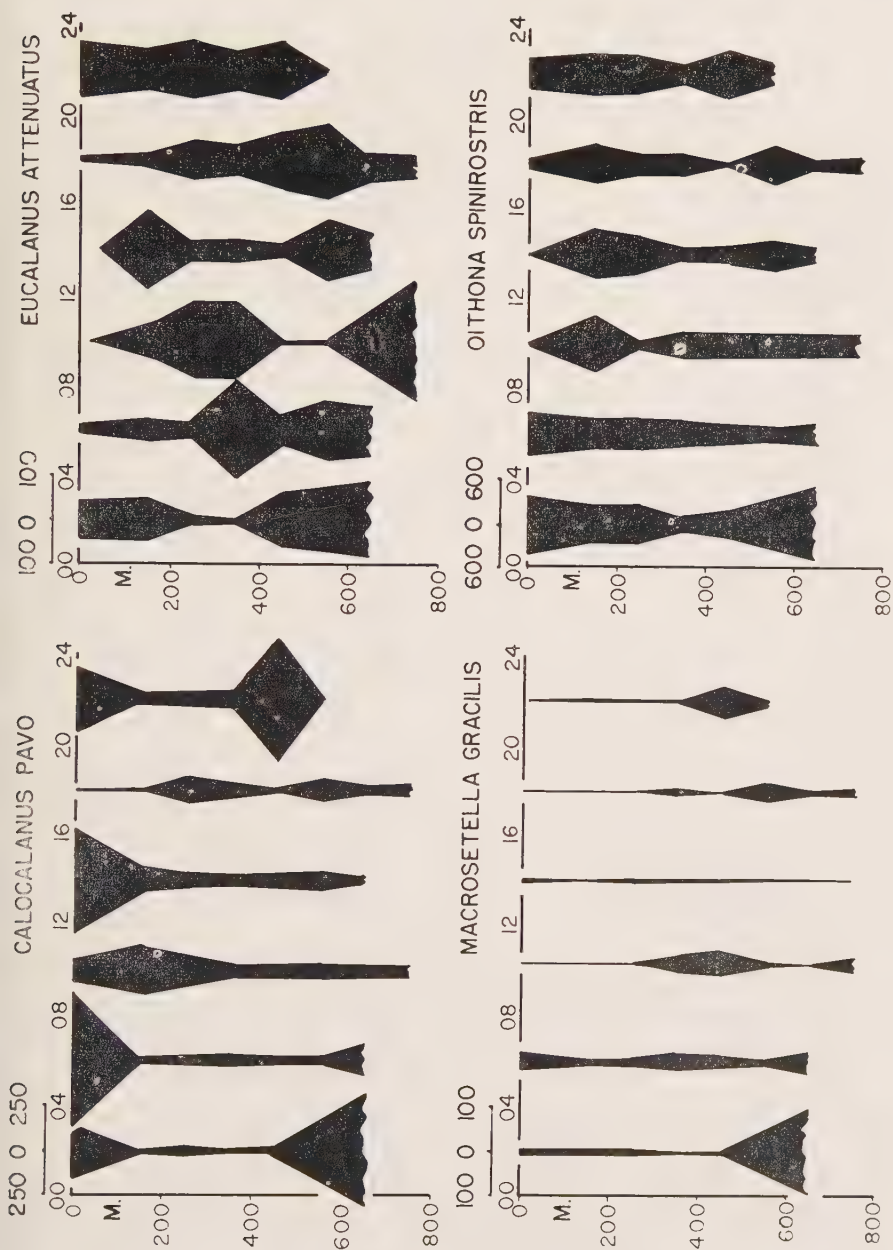


FIG. 3. Mean vertical distribution for the various species at the 40 mile station.

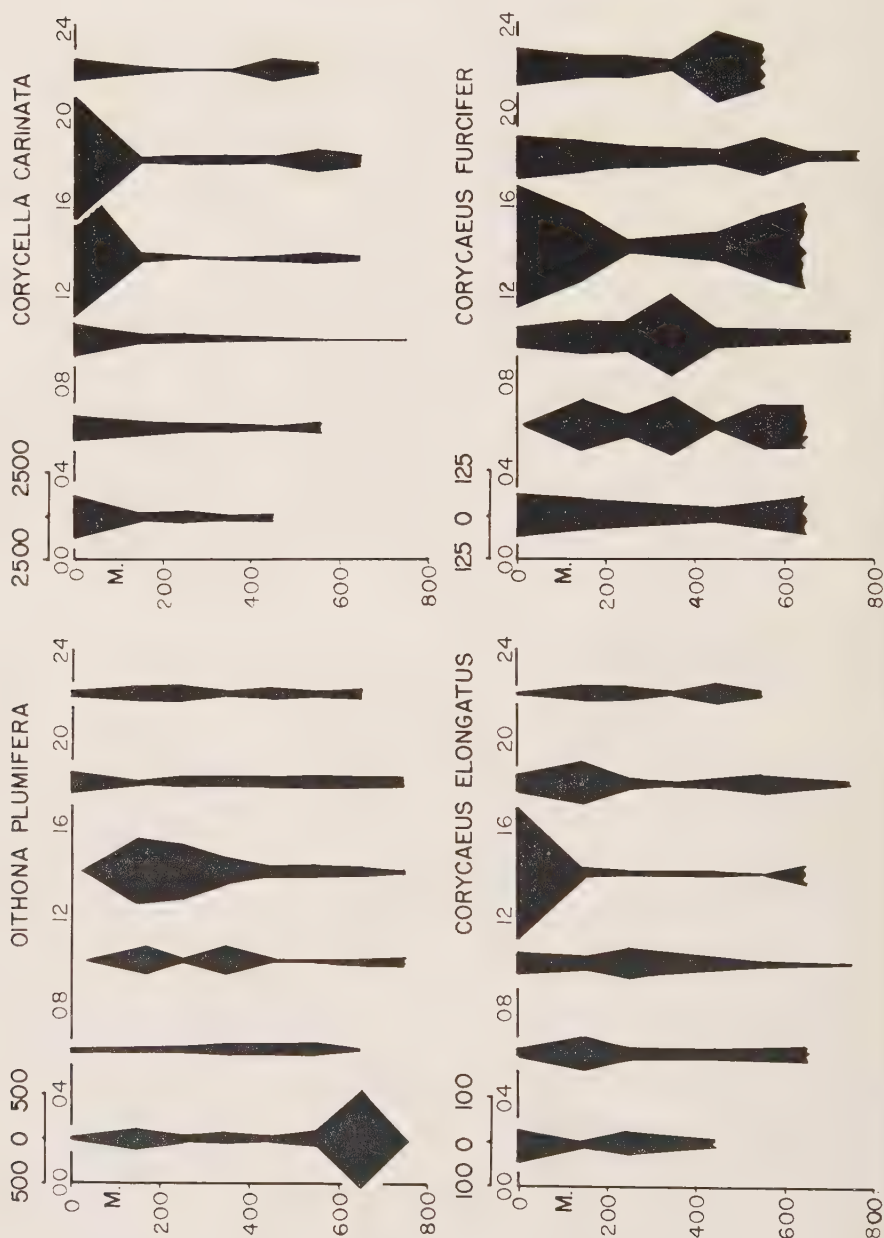


FIG. 4. Mean vertical distribution for the various species at the 40 mile station.

The Bermuda studies, which grouped together animals from many phyla, showed that deeper-living species performed a more extensive diurnal migration than shallower-living ones. Of 38 species, ten showed either no diurnal migration or a reversed one (that is up in the daytime and down at night). The night levels were, however, based on a single 24-hour station only. The results for the sixteen copepod

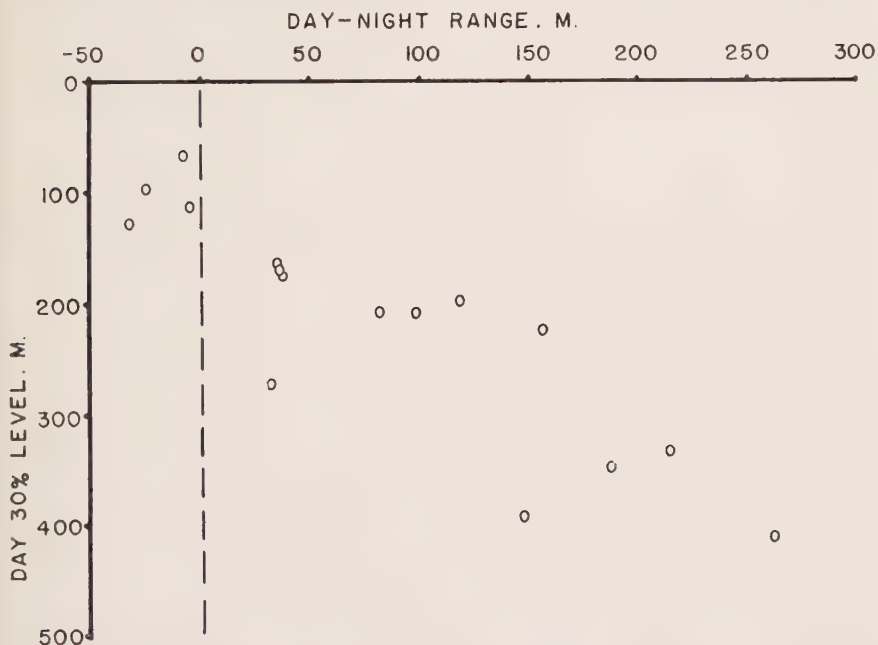


FIGURE 5. 40 mile station. The relation between the day-night range of the 30% level of each species and its day level. A negative value indicates a downward movement at night.

species in the present series, based on seven 24-hour stations at the 40-mile station, are shown in Fig. 5. The correlation between extent of migration and day level is clear, and four of the species show some downward movement at night, these being the four shallowest-living species.

THE RELATION BETWEEN DAY LEVEL AND ENVIRONMENTAL CONDITIONS

The Bermuda data on day levels were based on a more adequate series than those on the night levels. They showed that the vertical dispersion of a deep-living species was greater than that of a shallow-

living species. This spread was expressed as the vertical distance between the 25% and the 75% levels. The same effect was found in three out of four phyla of plankton studied in the Florida Current (Moore *et al.*, 1953). Another aspect of this correlation with depth is shown in Figs. 6 and 7. These show the range of temperature and illumination conditions over which the 30% level of each species was found at midday at all stations. The species are arranged in order of day level, and it is clear that the deeper-living ones spread over a much wider range of conditions than do the shallower-living ones. This applies only to the daytime.

NIGHT LEVEL

Although only one 24-hour station was worked in Bermuda, there was a good series of night surface hauls, made about midnight, from which it was shown that most species were more abundant at the surface at night at full moon than at new moon. Further, this correlation with moonlight was stronger in species which lived deep in the daytime than in shallower-living ones.

For the 40-mile station the midnight surface counts for each species from three moonless nights may be compared with those from four moonlit nights. If the results are expressed as the ratio of the mean surface count on moonlit nights to the mean surface count on dark nights, it is shown that for the six shallow-living species with little or no diurnal migration, or a reverse type, the mean ratio is 5.5; for the five intermediate species with moderate diurnal migration it is 4.3; and for the four deep-living species with extensive diurnal migration it is 1.9. The aberrant *Macrosetella gracilis* was never taken at the surface on the dark nights. The generally greater concentration at the surface on moonlit nights confirms the Bermuda results. However, the moonlight correlation is strongest in the deeper-living species in Bermuda and in the shallower-living species at the 40-mile station.

The mechanism which apparently gives this difference is complex. We can estimate the effect of moonlight on the population as a whole by comparing the 30% levels of the species on dark and moonlit nights. The ratio of dark to light levels is 1.3 in the shallower-living group of species, 0.6 in the intermediate group and 0.3 in the deep-living group. For *M. gracilis* it is 1.2. This series indicates that the center of concentration of the shallow-living species is higher on moonlit nights than on dark nights, with a resulting greater concentration at the surface. For the intermediate and deep-living species the center

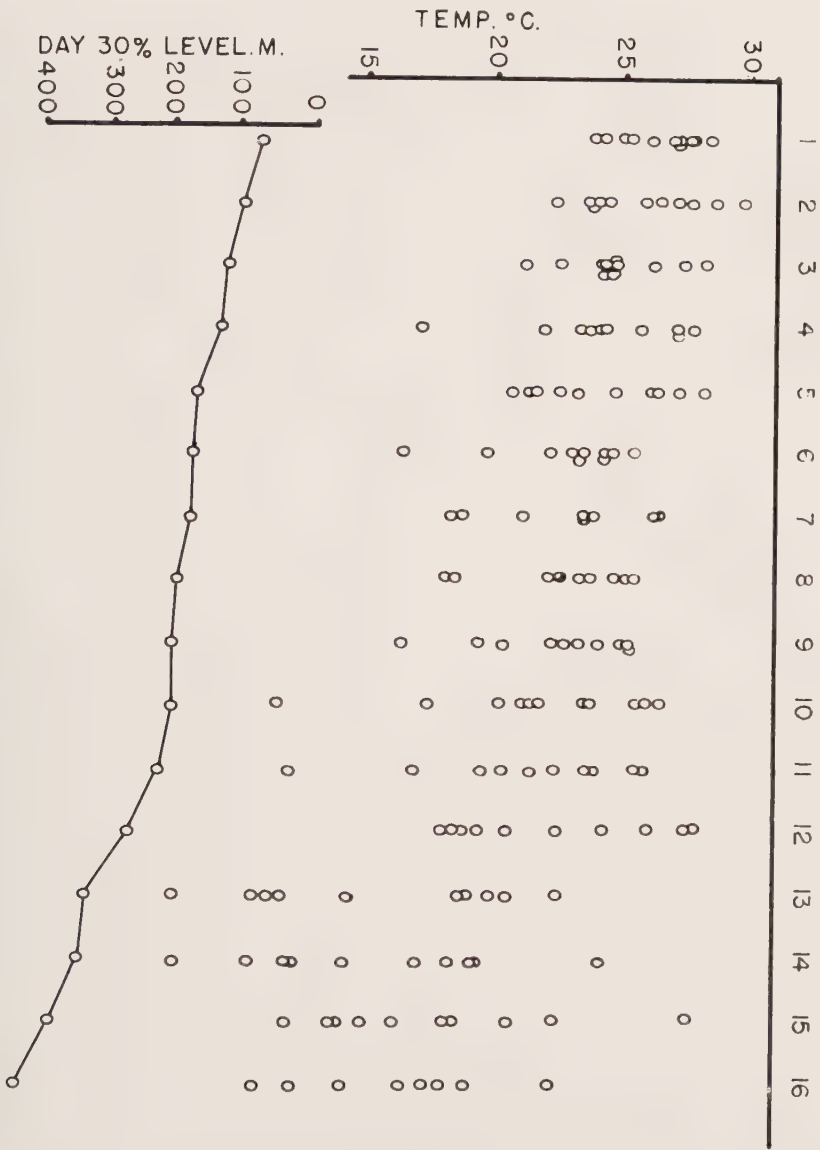


FIGURE 6. Data from all stations showing the temperatures at noon at the depth of the 30% level of the species. The species are arranged in order of their mean noon 30% levels, as shown in the lower graph.

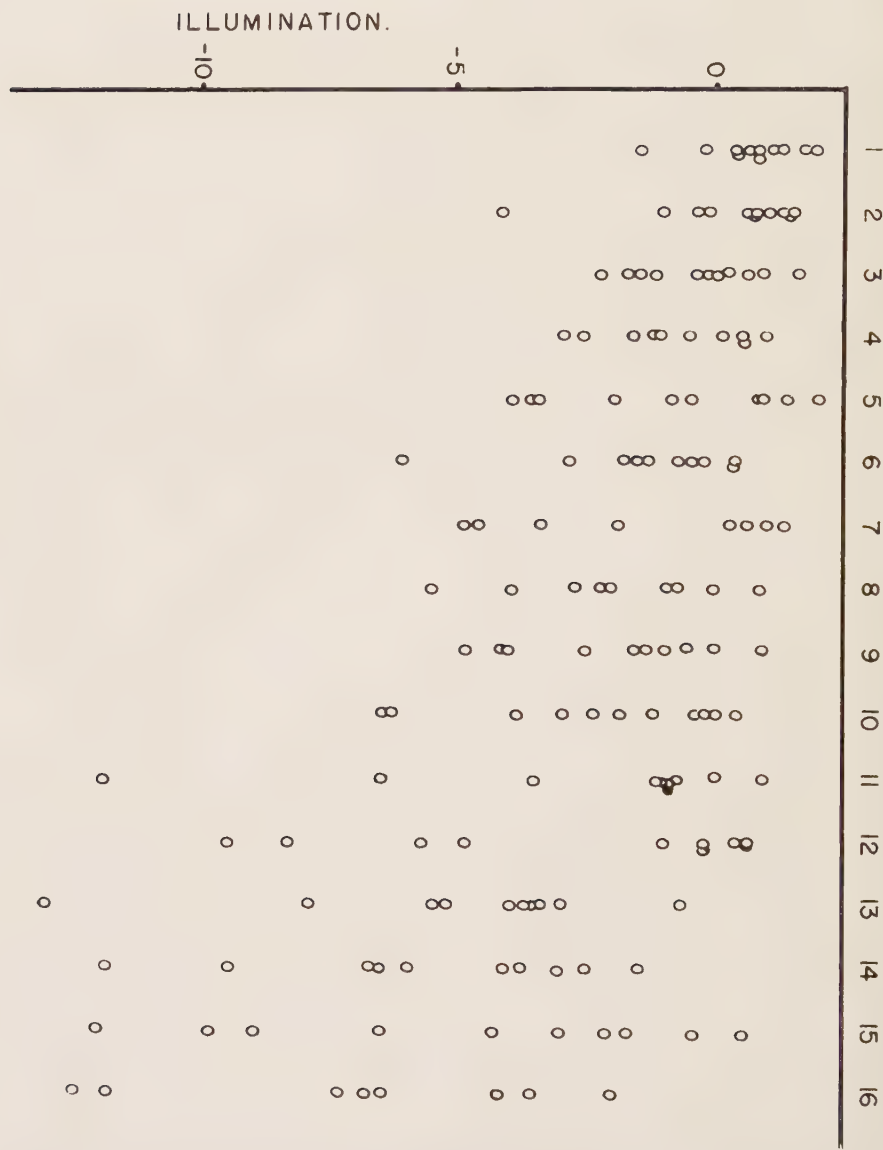


FIGURE 7. Data from all stations showing the illumination at noon at the depth of the 30% level of each species. The latter are in the same order as in Fig. 6.

of concentration is deeper on moonlit than on dark nights. Despite this, they are more abundant at the surface on the moonlit than on the dark nights, although the difference is less marked than in the shallow-living species. This may be interpreted as meaning that the deeper-living species are more diffuse vertically on moonlit than on dark nights with the result that, despite the downward movement of the center of concentration, they still have more individuals which reach the surface on moonlit nights than on dark nights. It will be remembered that the deep-living species are much more diffuse vertically in the daytime than are the shallow-living ones.

It seems likely that this difference between Bermuda and the 40-mile station in the relation between moonlight response and day level may lie in the considerable difference between day levels in the two places. From Table 2 it will be seen that there is such a difference in four of the five species from which comparable data are available.

TABLE 2
COMPARISON OF 50% DAY LEVELS (IN M) AT THE 40-MILE STATION
AND IN BERMUDA.

Species	40-mile station	Bermuda
<i>Calanus minor</i>	300	85
<i>Macrosetella gracilis</i>	332	70
<i>Pleuromamma gracilis</i>	434	> 300*
<i>P. abdominalis</i>	417	450
<i>P. xiphias</i>	500	> 300

* *P. gracilis* and *P. piseki* were not distinguished in obtaining this figure.

If this explanation is correct we should find that the Bermuda type of relationship occurs in that part of the Florida Current where the plankton characteristically lives shallower. This is the case, in fact, at the 10 and 15-mile stations. There are only four of these available, two with and two without moonlight, so the results may be considered only as a suggestion. For these stations, the ratio of light to dark night surface abundance is 3.1 in the shallow group, 13.4 in the intermediate group and 10.8 in the deep group, with *M. gracilis* having a value of 2.1. This series seems, therefore, to be consistent with Bermuda conditions.

THE REGULATION OF NIGHT LEVEL

In studies of the productivity in the Florida Current (Bsharah, in press), it has been shown that at night at the 40-mile station, the

greatest concentration of copepods, measured by displacement volume, is in the top 100 metres. By numbers, though, the maximum night concentration is between 100 and 200 metres. This difference between vertical distribution of volume and numbers is explained by the fact that most of those copepods which are close to the surface in the daytime are small species, while the larger ones, in general, live deeper. The present studies indicate that some of these small species move downwards at night whereas nearly all the larger ones move upwards.

If we plot the mean migration of the various species at the 40-mile station (Fig. 8), we find a noticeable tendency for the maximum concentration (30% level) of the various species studied to lie, at night, slightly below the 100 metre level regardless of the day level of the species. At this station, 100 metres represents the approximate depth of the euphotic zone throughout the year. It is rather surprising that most of the copepods should arrest their evening ascent just below the zone in which there is the maximum food production in the form of phytoplankton. Only about 30% of the population moves up into this zone.

If we combine the results from the 10, 15 and 40-mile stations, and plot for each species the temperatures at which the 30% levels lay on the various occasions, we obtain the results shown in Fig. 9. It is apparent that, although light plays a part in regulating night levels, temperature also is of major importance. The night temperatures are surprisingly constant, the mean values being close to 25°C. for all but the four deepest species and *M. gracilis*. For these it is about two degrees lower. Furthermore, there is no difference in temperature spread between the shallow and deep-living species. This is in strong contrast to the daytime conditions where the deeper-living species have progressively lower temperature means and greater temperature spreads (Fig. 5).

DISCUSSION

Both the diurnal migration of zooplankton and the differences in its vertical distribution under different hydrographic conditions, may play an important role in controlling horizontal and geographical distribution. Hardy and Gunther have proposed a mechanism which might allow the zooplankton to congregate in those concentrations of phytoplankton which best suit them. Dilwyn (1936) has shown how, in *Euphausia superba*, changes in vertical distribution with age

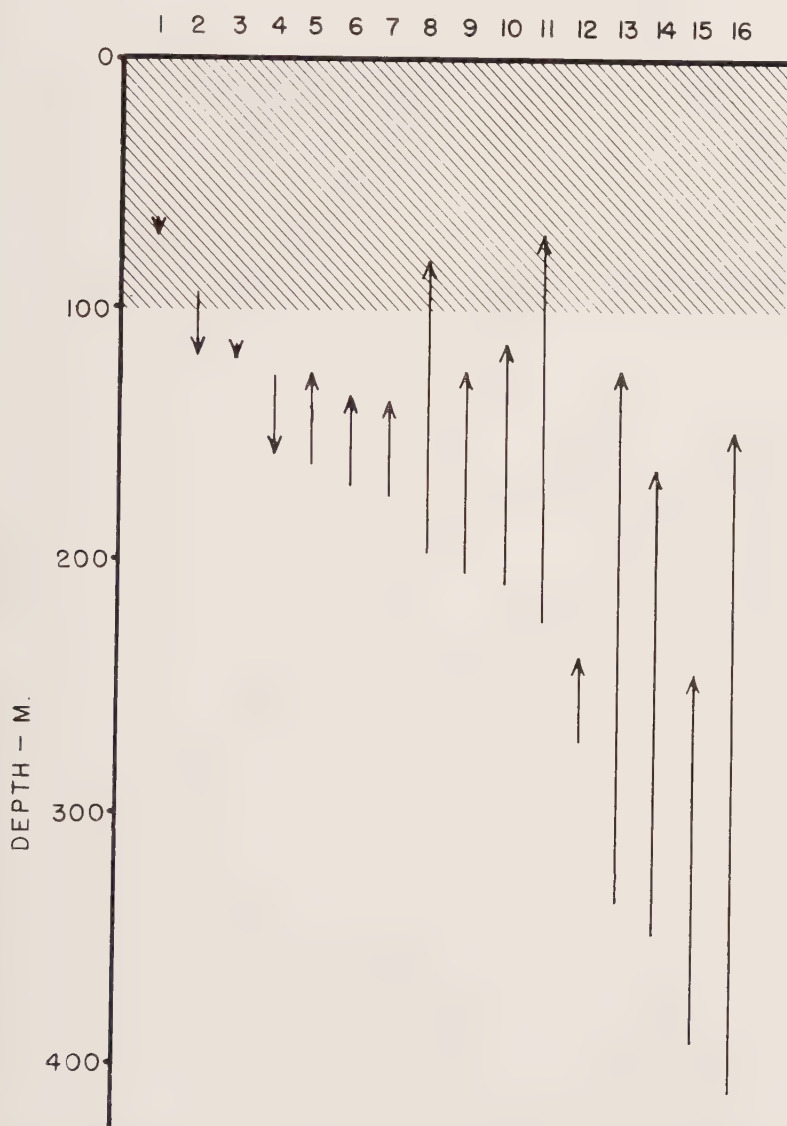


FIGURE 8. The mean values, at the 40 mile station, of the diurnal migration of the 30% level of the various species. The latter are arranged in the same order as in Fig. 6. Arrows indicate the direction of the evening migration and the hatched area approximately represents the euphotic zone.

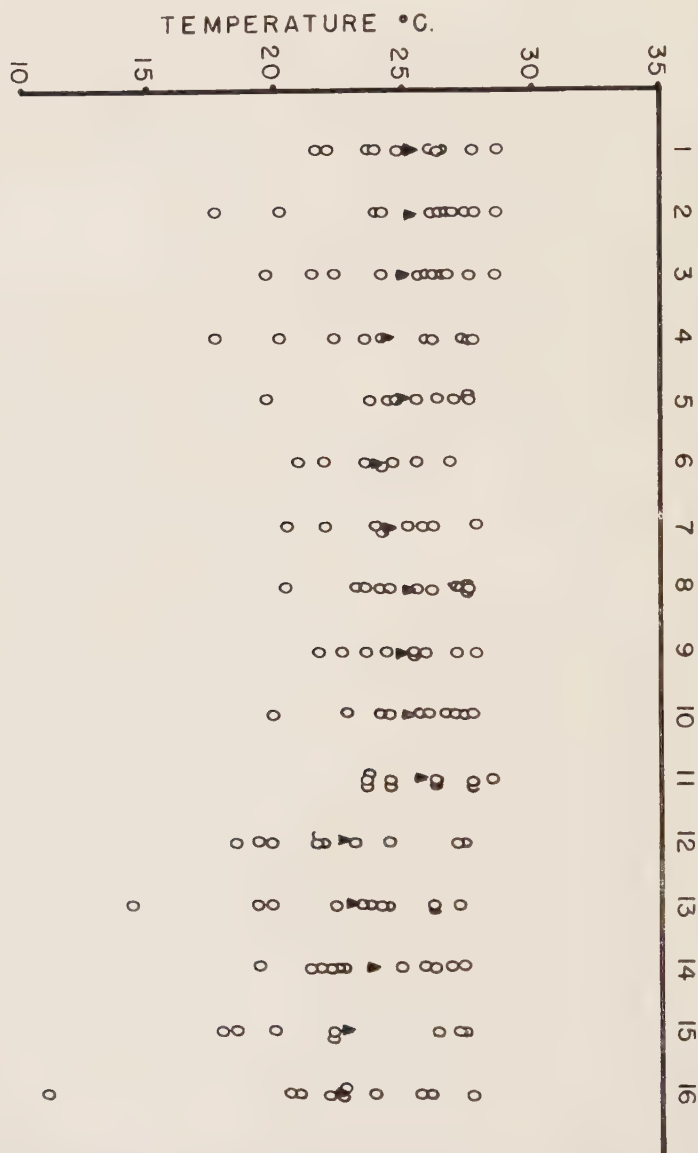


FIGURE 9. Data from all stations showing the temperatures at night at the 30% levels of the various species. The latter are arranged in the same order as in Fig. 6.

allow the species to take advantage of different current systems and so maintain a closed system of circulation in the Antarctic. Bousfield (1955) has demonstrated a similar situation with barnacle larvae in an estuary. Moore (1952) suggested that there might be two principal factors limiting the geographical distribution of euphausiids in the North Atlantic. One was the temperature encountered near the surface in the night ascent, and the other was a combination of light and temperature encountered during the day descent. The same general principles of level control seem to apply in widely differing animals (Moore, *et al.*, 1953), but there are undoubtedly specific differences in relative response to the different controlling environmental factors. An understanding of such specific differences may therefore be expected to help in understanding both large scale geographical distribution and also smaller scale irregularities of horizontal distribution.

One trend, found in various planktonic groups, and now confirmed in the copepods, is that deeper-living forms generally perform a more extensive diurnal migration than the shallower-living ones. This may appear obvious, but it has an important corollary. The deeper species must, in general, be able to tolerate a wider range and a more rapid fluctuation of temperature, pressure, and perhaps also illumination, than shallow species. This does not, of course, apply to still deeper forms which do not perform a diurnal migration, and for which conditions are relatively constant.

During the daytime, the deep-living species are more diffuse vertically than the shallow-living species. Further, the range of depths at which they concentrate varies more widely under different hydrographic conditions than it does in the shallow-living species. What is true of depth is true also of temperature and illumination. A population of a deep-living species comprises, on a given occasion, individuals tolerating a wider range of these conditions than a population of a shallow-living species. Further, the center of concentration (30% level) of a deep-living species will, on different occasions, be associated with a wider range of these conditions than that of a shallow-living species.

At night this pattern is completely changed. All species, regardless of their day level, show about equal diffuseness, and their depth is regulated chiefly by temperature and, secondarily, by light. The effectiveness of light in control of vertical distribution depends on whether the hydrographic conditions are such that all species tend to be deeper or shallower in the area in question. Where, as at the

40-mile station, all species tend to live deeper, it is the shallower-living species which are more responsive to light changes at night. Where all species tend to be shallower, as at the 10-15 mile stations and Bermuda, it is the deep-living species which are more responsive to night time levels of illumination. Behavior patterns, then, reflect not only the depth at which the animals typically live in the daytime, but also how this depth at which the species typically lives is modified by local conditions.

The marked temperature control at the night levels is of particular interest. In discussing the geographical distribution of euphausiids, Moore (1952) suggested that one geographical boundary might be set by the daytime conditions where the animals were forced either to endure too bright light or else to avoid it by descending into water too cold for them. The other boundary, set by conditions encountered during the night ascent, involved either encountering too warm water near the surface or else arresting their ascent at a lower level which would be cooler but which would be below the best feeding levels in the euphotic zone. There seems to be a definite tendency, in the Florida Current copepods, for the majority of the animals to stop their ascent just below the euphotic zone, and to do this under the control of temperature.

In this connection, and bearing in mind the similarity in behavior pattern which has been found in different groups (Moore, *et al.*, 1953), it is interesting to examine the temperature responses found in certain Florida Current siphonophores (Moore and Corwin, 1957). In this work, an estimate was made of the relative strengths of the responses to unit change in temperature, illumination and pressure. These responses change diurnally, and at midday the temperature response is weak relative to illumination, while at night the temperature response is relatively much stronger. A similar study has been completed for only one copepod, *Euchaeta marina*, but the same diurnal rhythm was found in this species also. It remains to be seen whether such diurnal rhythms differ in the various species, but the mean strengths of the temperature, and illumination responses seemed to be the same in the four species of siphonophores studied despite some difference in their day levels.

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THE RELATIONSHIP OF TOTAL PHOSPHORUS CONCENTRATION IN SEA WATER TO RED TIDE BLOOMS¹

SELWYN JACK BEIN

The Marine Laboratory, University of Miami

ABSTRACT

An examination of existing published and unpublished data concerning total phosphorus concentration before, during, and after Red Tide outbreaks was undertaken.

The literature and earlier data have indicated that abnormally high phosphorus content is frequently associated with plankton blooms. An examination of all available data reveals that this is not so in the case of Red Tide outbreaks off the west coast of Florida.

It was concluded that waters of the west coast of Florida maintain a sufficient phosphorus content to support a Red Tide at all times of the year and that fluctuations in this have no direct value in predicting outbreaks.

INTRODUCTION

The Marine Laboratory of the University of Miami, acting for the Florida State Board of Conservation, has been concerned with the task of attempting to forecast and control the phenomenon known as the Red Tide. As a necessary preliminary to this, part of the investigations has been directed to an understanding of the pattern followed by outbreaks, both geographically and in time, and to the relation of this pattern to readily observable ambient phenomena. Since the presence of unusually large concentrations of dissolved nutrients has usually been considered a necessary condition for this type of plankton bloom, special attention has been given to the nutrient conditions in the area, both during an outbreak and under "normal" conditions.

Brongersma-Sanders (1947) summarizes the opinions of a number of workers who have considered unusually high concentrations of nutrients as necessary prerequisites for a plankton bloom. In reference to discolored water accompanied by mass mortality of fishes off the west coast of Africa she states, "In my opinion the mortality is caused by noxiousness of red water dinoflagellates, the occurrence of red water in its turn being the result of the presence of upwelling water. On account of this upwelling, nutrients are available nearly all year round in high concentration. As a result the production of zoo/phytoplankton is excessively great."

Subsequent to the discovery of *Gymnodinium brevis* as the principal

¹Contribution No. 184 from The Marine Laboratory, University of Miami.

organism involved in the Florida Red Tide, and its description by members of The Marine Laboratory staff (Davis, 1948), attention was focused on the probable causes of its sporadic outbursts, and among these the possibility that the phosphorus content of seawater might be a controlling factor.

Walton Smith (1948) discussing the fundamental causes of the Florida west coast Red Tide reported, "It is therefore reasonable to assume that inorganic phosphorus is the principal factor limiting growth of phytoplankton in these waters at all times. This is in agreement with the general body of observations on tropical and sub-tropical waters. The great growth of organisms during the Red Tide must consequently be associated with a considerable increase in the nutrient phosphorus available." The opinions of Brongersma-Sanders and Smith reflect the hypothesis assumed by numerous other workers in the field, i.e., that abnormally large amounts of nutrients are necessary for a plankton bloom.

The presence of terrestrial deposits of mineral phosphorus in Florida and the suggestion that Red Tide outbreaks are related to rainfall (Marine Laboratory, 1954) gave rise to the belief that fluctuations in the rate at which phosphorus is leached from the land and drained to the coast might be related to Red Tide. Among others, Odum, *et al.* (1955) carried out analyses of river and drainage water associated with these deposits. Although no conclusive positive correlations were established by the various investigations, it was nevertheless considered desirable to compare the actual amount of total phosphorus present in the seawater of Red Tide areas during Red Tide outbreaks with that present at other times and places.

The data here considered are concerned only with total phosphorus concentrations. Inorganic phosphorus data have been ignored, since such values do not necessarily indicate the productive potentialities of sea water. They do not, in fact, usually show any direct or simple relation to the total amount of phosphorus or plankton present, and frequently, even, show an inverse relation to plankton growth.

Since the now accepted causative agent of Red Tide, *Gymnodinium brevis*, was not known until 1946 it was decided to use observations reported only after that date in order that the data would be restricted to those of fish kills unquestionably associated with this organism. It was decided therefore that comparative data for normal or non-Red Tide conditions be drawn from the same period. With the exception of some of Graham's offshore stations, data used are taken only from

those areas in which fish kills have been known to take place (Table 1).

TABLE 1
Sources of Total Phosphorus Data

Year	Area	Source
1948	Sarasota	Ketchum and Keen
1949-1950	Naples to Sarasota	Graham, <i>et al.</i>
1952	Fort Myers	Chew
1954	Gasparilla Island	Marine Laboratory
1954	Fort Myers to Gasparilla	Marine Laboratory
1954	Naples to Tampa	Lackey and Hynes
1955	Gasparilla Island	Marine Laboratory
1957	Fort Myers	U. S. Fish and Wildlife

METHODS OF CHEMICAL ANALYSIS OF SEAWATER

The Marine Laboratory water samples analyzed prior to January, 1954, were run according to the method of Redfield, *et al.* (1937). This consists of sulfuric acid-hydrogen peroxide digestion and a colorimetric estimation using ammonium molybdate and stannous chloride. In January, 1954 perchloric acid was substituted for sulfuric acid in digestion as a result of the work of Hansen and Robinson (1952). This method was used because perchloric acid is less contaminated with phosphorus than sulfuric and there is a more complete digestion of phosphorus compounds due to its higher oxidation rate. From January, 1955 to the present time ascorbic acid has been used in place of ammonium molybdate-stannous chloride because of its greater sensitivity as shown by recent work here (Greenfield and Kalber, 1955). Precautions were taken during the collection of all of the samples to avoid contamination and suitable reagent blanks were used in all cases.

Samples analyzed by the Woods Hole Oceanographic Institute and the University of Florida and referred to in this paper were accomplished by sulfuric acid-ammonium molybdate-stannous chloride techniques.

VALUES ASSOCIATED WITH ABSENCE OF RED TIDE

Sverdrup, Johnson, and Fleming (1942) state ". . . The maximum concentration of phosphorus to be expected at sea is about 2.0 microgram atoms per liter." Other values range from 0.0 to the above figure. Bruneau, Jerlov, and Koczy (1953) later revised this figure and reported a maximum of 3.5 microgram atoms per liter of *inorganic*

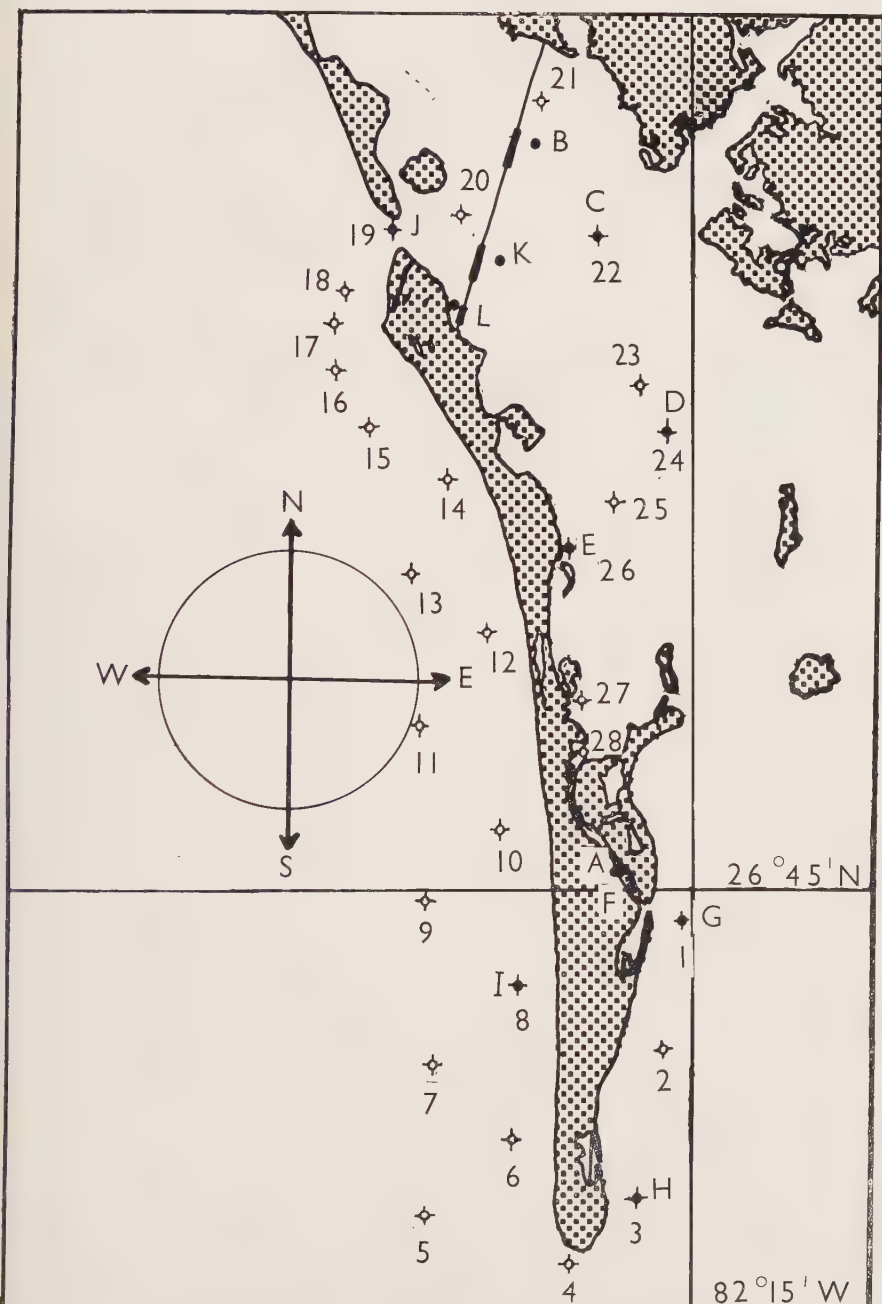


FIGURE 1. Location of 12 stations (lettered A to L) taken at Gasparilla Island during the Red Tide bloom of Dec. 1 and 2, 1954 and the location of 28 stations (numbered 1 to 28) taken from Aug. 29 to Oct. 10, 1955 during a period of no Red Tide.

TABLE 2

Total Phosphorus Readings of 98 Observations at 28 Stations
Taken at Gasparilla Island from August 29 to October 10, 1955
During a Period of no Red Tide

Date	Time Est.	Station Number	Total P. gA/L	Date	Time Est.	Station Number	Total P. gA/L
8-29	1335	1	2.43	9-10	1036	16	11.93
	1345	2	18.52		1043	18	16.34
	1350	3	2.02		1051	20	7.59
	1400	4	1.89		1117	22	8.31
	1408	5	2.18		1125	24	11.05
	1415	6	2.00		1130	26	15.95
	1420	7	1.97		1148	28	10.24
	1430	8	0.83		0950	1	15.28
	1437	9	2.34		1005	3	14.06
	1445	10	2.40		1012	5	24.72
	1452	11	2.05		1019	7	24.85
	1500	12	0.65		1026	9	25.60
	1510	13	2.11		1032	11	25.19
	1520	14	0.94		1042	13	22.06
	1530	15	3.99		1050	15	16.09
	1540	16	4.04		1055	17	25.33
	1547	17	1.73		1100	19	15.28
	1554	18	1.10		1109	21	27.16
	1604	19	2.67		1119	23	30.56
	1610	20	2.55	9-22	1129	25	26.82
9-12	1620	21	2.42		1138	28	15.28
	1650	22	13.22		0930	2	59.75
	1655	23	6.70		0940	4	35.31
	1700	24	4.84		0950	6	20.98
	1715	25	3.23		0957	8	46.17
	1720	26	2.19		1002	10	10.25
	1730	27	3.63		1010	12	13.22
	1740	28	7.43		1017	14	18.94
	1054	1	27.73		1025	16	10.39
	1105	3	26.61		1032	18	16.64
	1116	5	33.51		1040	20	24.79
	1122	7	8.80		1050	22	10.86
	1128	9	23.73		1100	24	22.47
	1135	11	26.12		1109	26	27.91
	1145	13	17.63		1115	28	28.78
	1154	15	16.82	10-10	0945	2	15.78
	1158	17	3.24		0955	4	18.41
	1205	19	24.02		1003	6	15.96
	1214	21	26.35		1010	8	21.39
	1224	23	24.85		1020	10	7.94
	1233	25	23.08		1029	12	15.35
	1242	27	19.96		1036	14	9.37
9-14	0928	2	21.98		1045	16	10.05
	0938	4	7.67		1050	18	10.66
	0949	6	30.87		1059	20	5.91
	1000	8	20.69		1110	22	17.86
	1007	10	10.73		1119	24	15.89
	1015	12	14.67		1125	26	17.79
	1023	14	11.29		1135	28	4.41

phosphorus at some deep stations in the Pacific Ocean. Although these values were inorganic no higher offshore values of inorganic or total phosphorus have been recorded.

Graham, *et al.* (1954) in a study made during 1949-50, reported total phosphorus values for thirteen stations on the west coast of Florida. Station 1 was located at Fort Myers at mid-channel on the

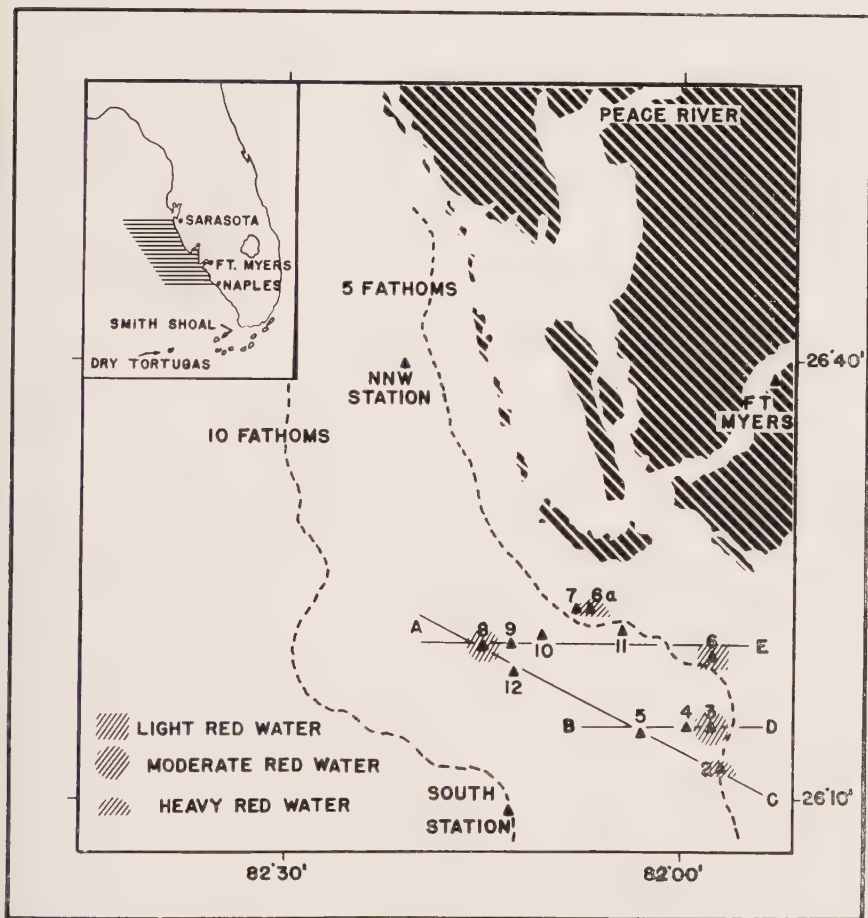


FIGURE 2. Locations of the 11 hydrographic stations (numbered 2 to 12), occupied in November, 1952. Stations with red water are indicated. Two stations occupied in 1949-1950 by Graham, *et al.*, are shown as NNW and South Stations. Inset map shows area of ocean covered by an airplane reconnaissance made in conjunction with the occupation of the 11 hydrographic stations. (From Chew, 1953).

Caloosahatchee River and Station 2 was at Punta Gorda in the mouth of the Peace River. These two stations represent a fresh water condition and will therefore be ignored. Stations 3 to 13 extend from Charlotte Harbor to a point 120 miles west of Gasparilla Island. They reported a range of total phosphorus readings from 0.00 microgram

TABLE 3

Total Phosphorus Values at Eleven Hydrographic Stations
Occupied in November 1952, off Fort Myers, Florida.
Red Tide Stations are in *Italics*. (After Chew, 1953).

Date Nov.	Station Number	Time EST	Depth (M)	Total Phosphorus microgram-at./L
<i>14</i>	<i>2</i>	<i>1451</i>	<i>0</i>	<i>2.3</i>
<i>14</i>	<i>2</i>	<i>1451</i>	<i>6</i>	<i>0.3</i>
<i>14</i>	<i>2</i>	<i>1451</i>	<i>10</i>	<i>1.7</i>
<i>15</i>	<i>3</i>	<i>1127</i>	<i>0</i>	<i>0.2</i>
<i>15</i>	<i>3</i>	<i>1127</i>	<i>5</i>	<i>0.7</i>
<i>15</i>	<i>3</i>	<i>1127</i>	<i>10</i>	<i>0.1</i>
<i>15</i>	<i>4</i>	<i>1240</i>	<i>0</i>	<i>0.6</i>
<i>15</i>	<i>4</i>	<i>1240</i>	<i>5</i>	<i>2.8</i>
<i>15</i>	<i>4</i>	<i>1240</i>	<i>10</i>	<i>0.7</i>
<i>15</i>	<i>5</i>	<i>1338</i>	<i>0</i>	<i>3.8</i>
<i>15</i>	<i>5</i>	<i>1338</i>	<i>6</i>	<i>2.0</i>
<i>15</i>	<i>5</i>	<i>1338</i>	<i>12</i>	<i>0.0</i>
<i>15</i>	<i>6</i>	<i>1600</i>	<i>0</i>	<i>2.4</i>
<i>15</i>	<i>6</i>	<i>1600</i>	<i>3</i>	<i>0.0</i>
<i>15</i>	<i>6</i>	<i>1600</i>	<i>7</i>	<i>0.7</i>
<i>16</i>	<i>6a</i>	<i>1154</i>	<i>0</i>	<i>0.5</i>
<i>16</i>	<i>6a</i>	<i>1154</i>	<i>3.9</i>	<i>1.1</i>
<i>16</i>	<i>6a</i>	<i>1154</i>	<i>7.9</i>	<i>0.6</i>
<i>16</i>	<i>7</i>	<i>1234</i>	<i>0</i>	<i>0.3</i>
<i>16</i>	<i>7</i>	<i>1234</i>	<i>4.9</i>	<i>1.3</i>
<i>16</i>	<i>7</i>	<i>1234</i>	<i>8.9</i>	<i>0.3</i>
<i>16</i>	<i>8</i>	<i>1408</i>	<i>0</i>	<i>1.0</i>
<i>16</i>	<i>8</i>	<i>1408</i>	<i>7</i>	<i>1.2</i>
<i>16</i>	<i>8</i>	<i>1408</i>	<i>12.9</i>	<i>1.6</i>
<i>16</i>	<i>9</i>	<i>1510</i>	<i>0</i>	<i>0.4</i>
<i>16</i>	<i>9</i>	<i>1510</i>	<i>6</i>	<i>0.2</i>
<i>16</i>	<i>9</i>	<i>1510</i>	<i>10.9</i>	<i>0.0</i>
<i>16</i>	<i>10</i>	<i>1655</i>	<i>0</i>	<i>0.5</i>
<i>16</i>	<i>10</i>	<i>1655</i>	<i>5</i>	<i>0.1</i>
<i>16</i>	<i>10</i>	<i>1655</i>	<i>10.9</i>	<i>0.3</i>
<i>17</i>	<i>11</i>	<i>1225</i>	<i>0</i>	<i>0.4</i>
<i>17</i>	<i>11</i>	<i>1225</i>	<i>3.9</i>	<i>0.5</i>
<i>17</i>	<i>11</i>	<i>1225</i>	<i>8.9</i>	<i>0.2</i>
<i>17</i>	<i>12</i>	<i>1407</i>	<i>0</i>	<i>0.1</i>
<i>17</i>	<i>12</i>	<i>1407</i>	<i>3.9</i>	<i>0.4</i>
<i>17</i>	<i>12</i>	<i>1407</i>	<i>9.8</i>	<i>0.6</i>

atoms per liter 120 miles west of Gasparilla Island to 4.40 microgram atoms per liter in Charlotte Harbor. During the period of their studies no Red Tide outbreaks were reported, even though the total phosphorus value at times exceeded the highest recorded from the phosphorus-rich water of deep ocean stations.

In the fall of 1955, a series of 98 observations were made around Gasparilla Island (Figure 1) by Marine Laboratory investigators. This study was conducted during a period in which no Red Tide had been reported for at least eight months. Nevertheless, an average total phosphorus reading of 14.74 microgram atoms per liter was recorded for these stations (Table 2). These figures ranged from approximately one fifth to eighteen times the maximum phosphorus values found at sea.

The U. S. Fish and Wildlife Service in a personal communication reports phosphorus values for the Fort Myers area during 1957, which were almost 30 times the maximum reported at sea, even though, at the time of their report, there had been no Red Tide outbreaks for more than two years.

VALUES ASSOCIATED WITH RED TIDE OUTBREAKS

Ketchum and Keen (1948) examined samples from a series of stations off Sarasota, Florida, both during and after the flowering of *Gymnodinium brevis*. At four stations containing red water they reported total phosphorus values of $2\frac{1}{2}$ to 10 times greater than the maximum figures given by Sverdrup, *et al.* (op. cit.) or about 1 to 5 times that of Bruneau, *et al.* (op. cit.) but well below the maxima reported off the coast of Florida in the absence of Red Tide.

Chew (1953) reported 36 observations at 11 hydrographic stations in the Fort Myers area during a period of Red Tide (Figure 2) and recorded an average total phosphorus reading for the surface red stations of 1.11 microgram atoms per liter (Table 3). From January, 1954 to June, 1954 the Laboratory made a series of observations from shore stations and aboard the Research Vessel T-19. Mr. Donald P. deSylva has prepared an interpolative graph of the relationship of total phosphorus to *Gymnodinium* populations from these data (see Figure 3). DeSylva's figures show a mean total phosphorus in red water considerably lower than many values in "normal" waters.

On December 1 and 2, 1954, an outbreak of Red Tide was reported at Gasparilla Island. A member of The Marine Laboratory staff made a series of observations at this time (see Figure 1). The mean phosphorus reading for the fifteen stations with the highest concentrations

of *G. brevis* was 4.46 microgram atoms per liter. The greatest amount of phosphorus recorded at that time was 18.21 microgram atoms per liter at a station containing no more than 16,000,000 *G. brevis* cells per liter (Table 4).

Lackey and Hynes (1955) report an analysis of 18 samples of Red Tide water, fifteen of which are below 0.5 microgram atoms per liter. Lackey and Sawyer (1945) give 0.5 microgram atoms of phosphorus (0.015 ppm) as necessary to support a plankton bloom. Lackey and Hynes (op. cit.) also report *G. brevis* populations as high as 4,814,000 cells per liter with no detectable phosphorus in the water. A personal communication from the senior author acknowledged that these samples were analyzed with the *G. brevis* cells in them.

The phosphorus values reported by Ketchum and Keen at the time of Red Tide although much higher than those reported for the open ocean and their "normal" stations are found to be considerably lower than many of the values reported by The Marine Laboratory at Gasparilla Island during a "normal" or non-Red Tide period (see Table 1). The values reported by Chew (op. cit.) for Red Tide blooms are also considerably lower than the "normal" mean reported at Gasparilla Island and in fact do not differ appreciably from the "normal" stations taken at the same time (see Table 2). Using only those of Chew's surface stations which definitely contained *G. brevis* and comparing them to the stations without red water it was found that the Red Tide stations ranged from 0.2 to 2.4 microgram atoms of phosphorus per liter with a mean of 1.11 as compared to a range of 0.1 to 3.8 microgram atoms of phosphorus per liter with a mean of 0.97 for the "normal" stations.

The values of DeSylva as shown in Figure 4 during Red Tide outbreaks are considerably below those during many non-Red Tide periods for the same locations and are not significantly different from his own values immediately preceding and following such outbreaks. The total phosphorus values reported at Gasparilla Island for December 1 and 2, 1954 during an active Red Tide are found to be considerably lower than some of the values for the same area eight months later at the same location.

The total phosphorus values of Lackey and Hynes (op. cit.) at eighteen Red Tide stations are considerably below the values at these locations during non-Red Tide periods and are in fact astonishingly low for any type of plankton bloom.

PHOSPHORUS CONTENT OF BLOOM ORGANISMS

Confirmatory evidence as to the order of magnitude of the minimum phosphorus concentration required to support a Red Tide outbreak may be deduced from the chemical analysis of planktonic organisms. In the absence of adequate samples of *G. brevis* at the time, a sample of mixed concentration nannoplankton was used, on the assumption that the phosphorus content would be of approximately the same order of magnitude as in *G. brevis*. A sample of 0.095 cc, measured by displacement, when dried, weighed 10.3 mg. The volume of a *G. brevis* cell was calculated from actual measurement to be approximately 7000 cubic microns. 0.095 cc is therefore equivalent to 13,500,000 cells and the dry weight of a single cell is $10.3/13,500,000$, or 0.75 mg for 10^6 cells.

The dry weight to carbon ratio as determined by Trask (1939) and the carbon phosphorus ratio of 54:1 determined by Fleming (1940), when applied to the dryweight equivalent of *G. brevis* gives a value of 0.25 microgram atoms of phosphorus for 10^6 cells. Since Harvey (1955) calculates the carbon phosphorus ratio as high as 108:1 in a phosphate deficient medium, the minimum value for total phosphorus content of a bloom becomes 0.125 microgram atoms per 10^6 cells.

Direct analysis of nannoplankton samples for total phosphorus gave a value of 0.5 microgram atoms for the volume equivalent of 10^6 cells of *G. brevis*. It may be concluded, therefore, that the minimum amount of total phosphorus in a Red Tide bloom of 10^6 cells per liter must be in the order of 0.1 to 0.5 microgram atoms per liter. This is similar to conclusions reached by Lackey and Sawyer (op. cit.) regarding the amount of phosphorus needed to support a plankton bloom.

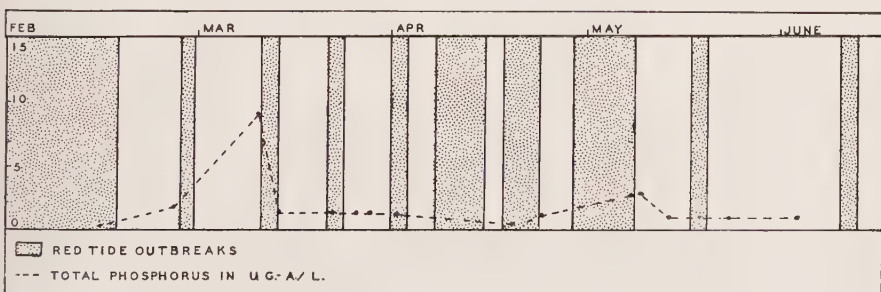


FIGURE 3. Interpolative graph showing the relationship of total phosphorus to Red Tide outbreaks for four and one half months of 1954 in the Fort Myers, Florida area. (After DeSylva).

Various workers have stated that, in Red Tide blooms, as few as 25,000 cells per liter may cause discolored water and death of fishes. The minimum concentration of phosphorus in such a bloom, according to the above calculations, would be of the order of magnitude of .01 microgram atoms per liter. Even in the unusual concentration of 20 million cells per liter found on one occasion (Table 4) the phosphorus concentration would only be in the order of magnitude of 10 microgram atoms per liter.

For average blooms, with organisms in concentrations of less than 1,000,000 cells per liter, the phosphorus content would be in the order of 0.4 microgram atoms per liter.

The order of magnitude of phosphorus concentration in an average Red Tide bloom, as here deduced, is considerably lower than the maximum figure for Florida west coast waters in "normal" years and well within the range of deep offshore waters.

TABLE 4
Total Phosphorus values and *Gymnodinium brevis* Counts
Taken at Gasparilla Island, December 1 and 2, 1954
During a Red Tide Outbreak

Station	Time EST	<i>G. brevis</i> (per liter)	Total Phosphorus (g-at./L.)
DECEMBER 1, 1954			
A	0830	2500	3.29
B	0900	4500-7500	1.81
B	0915	3500-6000	1.94
C	1000	300,000-400,000	1.74
D	1030	600,000-1,000,000	1.53
E	1100	500,000-600,000	1.65
F	1130	600,000-1,000,000	2.23
G	1200	300,000-400,000	2.19
A	1500	10,000,000-12,000,000	8.22
DECEMBER 2, 1954			
A	0800	0	3.30
G	0930	50,000-75,000	3.27
H	0945	60,000-100,000	2.97
I	1015	600,000-1,000,000	1.48
J	1030	200,000-400,000	1.60
K	1045	0	1.59
K	1100	600,000-1,000,000	1.73
L	1500	13,640,000-16,000,000	18.21
L	1700	20,000,000-25,000,000	11.87
L	2115	60,000-80,000	5.40
A	2115	60,000-100,000	2.86

DISCUSSION

The data examined clearly shows that total phosphorus values off the Florida west coast, though highly variable, are usually higher than in deep ocean waters, even in normal years. Fluctuations in these values are especially marked in the endemic Red Tide areas of Gasparilla Island and Fort Myers. A comparison of open ocean, Red Tide, and non-Red Tide total phosphorus values (Table 5) show many overlapping values and no indications of which of these values might represent a "typical" condition for *Gymnodinium* blooms.

In periods of Red Tide outbreaks the total phosphorus content of a bloom, including the organisms and particulate phosphorus, is lower than the maximum values recorded in "normal" years and, with the exception of Ketchum and Keen's values, is not significantly different from the adjacent areas with no Red Tide examined at the same period. At many times and places examined in the absence of Red

TABLE 5
Phosphorus Concentration in Relation to Red Tide

Year	Area	Total Phosphorus (g-at./L.)	Source
<i>PERIODS OF NO RED TIDE OUTBREAKS</i>			
1942	Offshore	2.0 (Max.)	Sverdrup
1953	Pacific, deep waters	3.5* (Max.)	Bruneau, et al.
1949-50	Gasparilla Island, Fla. to 120 miles offshore	4.40 (Max.)	Graham
1955	Gasparilla Island, Fla.	14.74 (Average)	Marine Laboratory
1957	Ft. Myers, Fla.	100.00 (Max.)	U.S.F.&W.S.
<i>PERIODS OF RED TIDE OUTBREAK</i>			
1948	Sarasota, Fla. Red Tide water	20.4 (Max.)	Ketchum & Keen
1948	Sarasota, Fla. "Normal" water	2.5 (Max.)	Ketchum & Keen
1952	Ft. Myers, Fla. Red Tide water (surface)	2.4 (Max.)	Chew
1952	Ft. Myers, Fla. "Normal" water (surface)	3.8 (Max.)	Chew
1954	Gasparilla Island, Fla. Red Tide water	4.46 (Average)	Marine Laboratory
1955	Same. (16×10^6 cells/liter)	18.21 (Max.)	Marine Laboratory
1955	Florida. Red Tide water	0.5 (Majority)	Lackey & Hynes

*Expressed as inorganic.

Tides or blooms, Florida west coast waters contained at least as much and often more than the estimated order of magnitude of total phosphorus contained in a heavy plankton bloom. The total phosphorous values of Lackey and Hynes (op. cit.) for Red Tide stations, which were analyzed with the organisms in the samples, are unusually low for any type of plankton bloom and there is no obvious explanation for these figures.

CONCLUSION

An examination of total phosphorus content before, during, and after a Red Tide outbreak leads to the conclusion that phosphorus is not a limiting factor for *Gymnodinium brevis* blooms on the Florida west coast. It is possible that the threshold level of total phosphorus necessary to support dense populations of this organism is lower than originally assumed. The fact that the waters under consideration are usually rich in this mineral has perhaps led to much of the confusion in dealing with this problem. It seems very probable that, insofar as phosphorus is concerned, the areas of the west coast of Florida which have recorded Red Tides are, at all times, capable of supporting an outbreak. Since the total phosphorus content may no longer be considered a limiting factor here it has no value in predicting outbreaks.

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LITERATURE ON HALOPHILOUS AND HALOLIMNIC FUNGI¹

T. W. JOHNSON, JR.

Department of Botany, Duke University

AND

SAMUEL P. MEYERS

The Marine Laboratory, University of Miami

ABSTRACT

A bibliography of references to publications on marine and brackish water fungi, together with annotations on some articles, is presented. The references are world-wide in scope, and include all phases of marine mycology.

INTRODUCTION

Since the turn of the present decade, a considerable interest in marine fungi has developed, evidenced by the increasing number of publications. In some instances the papers are not readily available, yet are significant in terms of their contribution to the morphology, ecology, physiology, and taxonomy of marine fungi. Literature previous to 1950, similarly, is scattered throughout numerous journals, some having limited distribution. Furthermore, significant reports of marine or brackish water fungi may be overlooked, especially if they represent only a minor portion of broad taxonomic monographs or compilations of species.

Considering the paucity of work previously done on marine fungi, in comparison with the vast literature extant on terrestrial and fresh water fungi, it is evident that the field of marine mycology is yet in its infancy. It seems justified, therefore, to make available now as complete a bibliography as possible so that future workers will have basic references available to them. Particularly in taxonomic studies, at present far from static, the need for a bibliography is imperative. To some extent, at least, unnecessary and confusing duplication of descriptions, and lengthy synonymy, may be avoided.

The subsequent bibliography, including brief abstracts of publications whose titles are not self-explanatory, is an attempt to bring together in one source the literature on marine and brackish water fungi. Portions of certain abstracts, enclosed in parentheses (), represent our interpretation of subject matter, or are notes added either for clarity or for indicating important changes in concepts expressed by other authors. A few references are included that do not deal with marine or brackish water fungi, yet are significant in their bearing on

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taxonomic problems with these fungi or protozoa-like parasites. Some references have undoubtedly been overlooked. A very few are not cited because of insufficient information about date, title, and journal, or incorrect citations in the publications from which the references were obtained. Several citations to papers dealing with fungi that are very questionably marine or brackish water forms (such as those occurring on beach-inhabiting phanerogams) are excluded. With a few exceptions, references to marine lichens are not included.

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Errors of omission or commission, brought to our attention, will be appreciated.

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1955. Marine fungi from Queensland—I. Papers, Univ. Queensland Dept. Bot., 3 (10): 77-81. [*Metasphaeria australiensis*, *Lulworthia longispora*, n. spp.; *Halophiobolus* shown to be antedated by Sutherland's genus *Lulworthia*; 2 Fungi Imperfecti reported.]

1956. Marine fungi from Queensland—II. Papers, Univ. Queensland Dept. Bot., 3 (12): 97-105. [*Haloguignardia* proposed as n. gen. for marine spp. of *Guignardia*. Two n. spp. *Haloguignardia*; 2 n. spp. *Halosphaeria* and one new comb., *H. trifurcata* (Höhnk's *Arenariomyces trifurcatus*); one n. sp. each *Ophiobolus* and *Gnomonia*. Two other known spp. reported.]

CROUAN, P. L. AND H. M. CROUAN

1867. Florule du Finistère. 262 pp. Brest and Paris. [*Sphaeria corallinarum* on *Corallina officinalis* and *Jania corniculata* (p. 24).]

DANGEARD, P. A.

- 1890-91. Contribution à l'étude des organismes inférieures. Le Botaniste, 2: 1-58. [*Olpidium aggregatum* (an imperfectly known sp., according to Sparrow, 1943).]

1912. Recherches sur quelques algues nouvelles ou peu connues. Le Botaniste, 12: 1-21. [*Olpidium marinum* mentioned and described briefly.]

1932. Observations sur la famille des Labyrinthulées et sur quelques autres parasites des *Cladophora*. Le Botaniste, 24: 217-258. [*Achlyogeton salinum* n. sp. (according to Sparrow, 1943, is probably *Siroldidium bryopsidis*); *Entophlyctis maxima*; *Labyrinthula chattonii* n. sp.]

DANGEARD, PIERRE

1934. Sur la présence à Roscoff d'une Chytridiale parasite des Ectocarpées, l'*Eurychasma Dicksonii* (Wright) Megnus. Ann. Protistol., Paris, 4: 69-73.

DANIEL, G. E.

- 1933a. Studies on *Ichthyophonus hoferi*, a parasite of the herring, *Clupea harengus*. I. The parasite as it is found in the herring. Amer. Jour. Hyg., 17: 262-276.

- 1933b. Studies on *Ichthyophonus hoferi*, a parasitic fungus of the herring, *Clupea harengus*. II. The gross and microscopic lesions produced by the parasite. Amer. Jour. Hyg., 17: 491-501.

DAVID, H. M.

1943. Studies in the autecology of *Ascomyllum nodosum* Le Jol. Jour. Ecol., 31: 178-198. [Mention of *Mycosphaerella ascomyilli*.]

DAVIDSON, R. W., FRANCES LOMBARD AND R. R. HIRT

1947. Fungi causing decay in wooden boats. Mycologia, 39: 313-327.

[Twenty wood-rot fungi isolated or collected from decayed wood from boats in various coastal cities and towns; terrestrial fungi only.]

DAVIS, H. C. AND V. L. LOOSANOFF

1954. A fungus disease in bivalve larvae. Proc. Natl. Shellfisheries Assn., 45: 151-156. [Fungus in clam and oyster larvae, tentatively described as a species of *Sirolopidium*; (described under specific epithet *zoophthorum* by Vishniac, 1955d).]

DAVIS H. C., V. L. LOOSANOFF, W. H. WESTON AND C. MARTIN

1954. A fungus disease in clam and oyster larvae. Science, (N. S.), 120: 36-38. [(First published report in detail of fungus described by Vishniac, 1955d, as *Sirolopidium zoophthorum*.)]

DECKENBACH, C. VON

- 1902-03. *Coenomyces consuens*, n. g., n. sp. Scripta Bot. Horti Univ. Imper., Petro., 19: 1-42. [*Coenomyces* in marine *Calothrix*.]
1903. *Coenomyces consuens* n. g., n. sp. (ein Beitrag zur Phylogenie der Pilze.) Flora, 92: 253-283.

DUBOSCQ, O.

1921. *Labyrinthomyxa sauvageau* n. g., n. sp., Protéomyxée parasite de *Laminaria Lejolisii* Sauvageau. Comptes Rendus, Séances et Mém. Soc. Biol., Paris, 84: 27-33.

DUBOSCQ, O., L. LÉGER AND O. TUZET

1948. Contribution à la connaissance des Eccrinides: les Trichomycètes. Arch. Zool. Exp. Gén., 86: 29-144. [Eccriniales in marine animals.]

DUCHASSAING DE FONBRESSIN, P. AND G. MICHELOTTI

1864. Spongiaires de la Mer Caraïbe. Maatts. Nat. Verh., Haarlem, Holland, 21: 1-124. [Report on fungus filaments in sponges.]

DUNCAN, P. M.

1876. On some Thallophytes parasitic within recent Madreporaria. Proc. Royal Soc., London, 25: 238-256. [Organisms under fungus epithets, *Achlya penetrans* and *Saprolegnia ferax*, described as occurring in molluscs. (Both organisms are probably boring siphonaceous algae.)]
1881. On some remarkable enlargements of the axial canals of sponge spicules and their causes. Jour. Royal Micr. Soc., (Ser. 2), 1: 557-572. [Mentions similarity of borings in spicules to *Achlya penetrans*; suggests the enlargements of spicule canals are probably due to "lowly organised plants."]

DURIEU DE MAISONNEUVE, C.

1846. Flore d'Algérie. Pyrénomycètes avec le concours de Montagne. In Montagne, Sylloge generum specierumque Cryptogamarum, Paris, pp. 443-600. [*Sphaeria posidoniae*.]

ELLIS, J. B. AND B. M. EVERHART

1885. New fungi. Jour. Mycol., 1: 148-154. [*Ophiobolus medusa* (synonymous with *Halophiobolus medusa* Linder, in Barghoorn and Linder, 1944, and with *Lulworthia medusa* Cribb and Cribb, 1955); species of *Leptosphaeria* (caulogenous).]
1892. The North American Pyrenomycetes. Publ. by the authors. [Descriptions of previously known brackish water or intertidal, caulogenous Pyrenomycetes, such as in the genus *Leptosphaeria*.]

ELLIS, MARJORIE F.

1928. *Ichthyophonus hoferi* Plehn & Mulsow, a flounder parasite new to North American waters. Proc. Trans. Nova Scotian Inst. Sci., 17 (3):

- 185-192. (1928-1929). [First report of organism in salt water; description; infection experiments.]
1929. Investigations on the protozoan fish parasites of the Saint Andrew's region. Proc. Trans. Nova Scotian Inst. Sci., 17 (4): 268-275. (1929-1930). [*Ichthyophonus hoferi* reported as protozoan; structure and habit described.]
- ESTEE, LULA M.
1913. Fungus galls on *Cystoseira* and *Halidrys*. Univ. California Publ. Bot., 4: 305-316. [*Guignardia irritans*.]
- FARLOW, W. G.
1875. List of the marine algae of the United States, with notes on new and imperfectly known species. Proc. Amer. Acad. Arts & Sci., (N. S.), 2: 351-380. [Comments, p. 378, on Harvey's *Blodgettia confervoides*.]
1881. Marine algae of New England and adjacent coasts. Rept. U. S. Fish Commission for 1879. [Mention, p. 10, of a *Sphaeria* parasitic on *Laminaria longicruris*.]
- FELDMANN, GENEVIÈVE
1953. La végétation de l'étang de Salses (rive sud). Vie et Milieu, 4: 685-700. [Mention of *Plasmodiophora bicaudata* on *Zostera nana*.]
1956. Développement d'une Plasmodiophorale marine: *Plasmodiophora bicaudata* J. Feldm., parasite du *Zostera nana* Roth. Rev. Gén. Bot., 63: 390-420.
- FELDMANN, J.
1931. Contribution à la flore algologique marine de l'Algérie. Les Algues de Cherchell. Bull. Soc. d'Hist. Nat. l'Afrique du Nord, 22: 179-254. [Marine fungus (similar to *Melanopsamma tregoubovii*) observed and reported, but not described.]
1932. Sur la répartition dans la Méditerranée occidentale du *Melanopsamma tregoubovii* Olliv. var. *cystoseirae* Olliv., Pyrénomycète parasite du *Cystoseira abrotanifolia*. Rev. Algol., 6: 225-226.
1936. Les Monocotylédones marines de la Guadeloupe. Bull. Soc. Bot., France, 83: 604-613. [A marine *Plasmodiophora* similar to *P. halophilae*.]
1937. Sur les gonidies de quelques *Arthopyrenia* marins. Rev. Bryol. Lichénol., (N. S.), 10: 64-73. [Discussion of *Epicymatia balani*, and relation to marine arthopyrenias.]
1938. Le *Blodgettia confervoides* Harv. est-il un Lichen? Rev. Bryol. Lichénol., (N. S.), 11: 155-163. (1939). [Fungus symbiotic with *Cladophora fuliginosa* named *Blodgettomyces borneti* (Wright). Plant is designated as the lichen *Cladophora fuliginosa-Blodgettomyces borneti*.]
1940a. *Maireomyces*, nouveau genre de Pyrénomycète marin. Bull. Soc. d'Hist. Nat. l'Afrique du Nord, 31: 163-166. [*M. peyssonelliae* n. sp.]
1940b. Une nouvelle espèce de Sphéropsidée parasite d'une algue marine. Bull. Soc. d'Hist. Nat. l'Afrique du Nord, 31: 167-170. [*Macrophoma gymnogongri*.]
1940c. Une nouvelle espèce de *Plasmodiophora* (*P. bicaudata*) parasite du *Zostera nana* Roth. Bull. Soc. d'Hist. Nat. l'Afrique du Nord, 31: 171-177.
1954. Inventaire de la flore marine de Roscoff. Supplément 6, Trav. Sta. Biol., Roscoff, 152 pp. [Lists, pp. 131-137, marine members of

Labyrinthula, Phycomycetes, Eccrinales, and Euascomycetes; marine lichens listed.]

FELDMANN, J. AND GENEVIÈVE FELDMANN

1940. Note sur une Chytridiale des spores de Cérarniacées. Bull. Soc. d'Hist. Nat. l'Afrique du Nord, 31: 72-75. [*Petersenia lobata*.]

1955. Observations sur quelques Phycomycètes marins nouveaux ou peu connus. Rev. Mycologique, (N. S.), 20: 231-251. [*Ectrogella eurychasmoides* and *Olpidiopsis magnusii*, n. spp.; *Ectrogella marina* comb. nov. (*Olpidiopsis marinum* Dangeard, 1912); biological observations on host specificity and reaction of host to parasite.]

FERDINANSEN, C. AND O. WINGE

1913. *Plasmodiophora Halophilae* sp. n. Centralbl. Bakteriöl., Parasitenk. Infektionskrankh., Abt. 2, 37: 167.

1914. *Ostenfeldiella*, a new genus of Plasmodiophoraceae. Ann. Bot., London, 28: 643-649. [*O. diplantherae*.]

1920. A *Phyllachorella* parasitic on *Sargassum*. Mycologia, 12: 102-103. [*P. oceanica*.]

FISCHER, A.

1892. Phycomycetes. Die Pilze Deutschlands, Oesterreichs, und der Schweiz. In Rabenhorst. Kryptogamen-Fl., 1 (4): 1-490. [Marine chytrids (often under names considered synonyms by Sparrow, 1943); *Olpidium entosphaericum* n. sp.]

FISCHER, B.

1894. Die Bakterien des Meeres nach den Untersuchungen der Plankton-Expedition unter gleichzeitiger Berücksichtigung einiger älterer und neuerer Untersuchungen. Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, 4: 1-83. ["*Torula*" spp. reported from northern and southern Atlantic.]

FISCHER, B. AND C. BREBECK

1894. Zur Morphologie, Biologie, und Systematik der Kahmpilze, der *Monilia candida* Hansen und des Soorerregers. G. Fischer: Jena. [Marine yeast, suggestive of *Sporobolomyces*.]

FISCHTHAL, J.

1944. Observations on a sporozoan parasite of the eelpout, *Zoarces anguillaris*, with an evaluation of candling methods for its detection. Jour. Parasit., 30: 35-36. [Describes a parasite in genus *Ichthyosporidium* (fungus). (According to Sproston, 1944, suggests *I. hoferi*.)]

FISH, F. T.

1934. A fungus disease in fishes of the Gulf of Maine. Parasitology, 26: 1-16. [*Ichthyosporidium hoferi*; historical aspects and bibliography.]

FRANK, M. AND E. HESS

1941a. Studies on salt fish. V. Studies on *Sporendonema epizoum* from "dun" salt fish. Jour. Fish. Res. Bd., Canada, 5: 276-286. [Morphological and physiological study; fungus is halophilic.]

1941b. Studies on salt fish. VI. Halophilic brown molds of the game *Sporendonema emend.* Ciferri et Redaelli. Jour. Fish. Res. Bd., Canada, 5: 287-292. [Cultural studies on 19 isolates of *S. epizoum*; compared for halophilism, temperature and pH limits, nutrition.]

GAIN, L.

1912. La flore algologique des régions antarctiques et subantarctiques. Deuxième Expedit. Antarct. Française (1908-1910). Paris. [Illustra-

tions of a *Macrophoma* in *Curdiaea roscovitzae* Hariot. (Feldmann, 1940b, suggests this is a n. sp., *M. antarctica*.)]

GALTISOFF, P. S.

1940. Wasting disease causing mortality of sponges in the West Indies and Gulf of Mexico. Proc. 8th Amer. Sci. Cong., 3: 411-421. [Suggests disease caused by coenocytic fungus tentatively placed in *Spongiphaga*; wool, velvet, grass, yellow, hardhead, and reef sponges infected.]

GALTISOFF, P. S., H. H. BROWN, C. L. SMITH AND F. G. WALTON SMITH

1939. Sponge mortality in the Bahamas. Nature, 143: 807-808. [Fungus filaments in diseased sponge tissue.]

GIARD, A.

1888. Sur les *Nephromyces*, genre nouveau de champignons parasites du rein des Mclgulidéés. Comptes Rendus Acad. Sci., Paris, 106: 1180-1182. [*N. roscovitanus*.]

GOEBEL, K.

1884. *Tetramyxa parasitica*. Flora, 67: 517-521. [Parasite on marine phanerogams.]

GRAN, H. H.

1900. Bemerkungen über einige Planktondiatomeen. Nyt. Mag. Naturvid., Christiania, 38: 105-128. [Describes *Olpidium lauderiae*. (Questionable validity according to Sparrow, 1943; probably synonymous with *Ectrogella perforans*, Aleem, 1953.)]

GRIGGS, R. F.

1912. The development and cytology of *Rhodochytrium*. Bot. Gaz., 53: 127-173. [(Figures suggest the fungus described by Kibbe, 1916, on *Alaria*, in which case are those of alga cystidia.)]

GUSTAFSSON, ULLA AND N. FRIES

1956. Nutritional requirements of some marine fungi. Physiologia Plantarum, 9: 462-465.

GWYNNE-VAUGHAN, H. I. C. AND B. BARNES

1937. The structure and development of the fungi. 2nd. Ed., Cambridge. [Places *Ichthyosporidium hoferi* in Entomophthoraceae (pp. 147-148).]

HARANT, H.

1931. Contribution à l'histoire naturelle des ascides et de leurs parasites. Ann. Inst. Océanogr., Monaco, 8: 231-389. [On *Nephromyces* in ascidian kidneys.]

HARDER, R. AND ESTHER UEBELMESSER

1955. Über marine saprophytische Chytridiales und einige andere Pilze vom Meeresboden und Meeresstrand. Arkiv Mikrobiol., 22: 87-114. [Twenty-five chytridiaceous species and unnamed Mucorales, Saprolegniaceae, and pythiums reported from soil under sea water, intertidal zones, beach dunes, and near pilings. Numerous fungi described as septate or nonseptate also reported. Several chytridiaceous fungi previously known from fresh water or terrestrial habitats are reported. Ecological aspects.]

HARIOT, P.

1887. Note sur le genre *Mastodia*. Jour. de Bot., 1: 231-234. [*Mastodia* (*Ulva tessellata*) reported to be an alga; "fruitings" of alga are fungus perithecia; *Epicymatia balani* Winter described.]

1889. Champignons. Algues. Mission scientifique du Cap Horn, 1882-1883, Vol. 5, Botanique. [*Amphisphaeria biturbinata* described; *Plecopara herbarum* on *Laminaria* and *Chondrus*, and *Eurychasma dicksonii* are reported.]
- HARIOT, P. AND N. PATOUILLARD
1904. Description de champignons nouveaux de l'Herbier du Muséum. Bull. Soc. Myc., France, 20: 61-65. [*Zignoella cubensis* n. sp.]
- HARVEY, W. H.
1858. Nereis Boreali-Americana: Contributions to the history of the marine algae of North America. Part III.—Chlorospermeae. Smithsonian Contrib. to Knowledge, 10: 1-140. [Describes, as marine alga, *Blodgettia confervoides* n. sp. (Illustrations show an innermost "cell coat" which suggests hyphal swellings, conidia, or chlamydospores of a fungus.)]
- HAUCH, F.
1878. Notiz über *Rhizophyidium Dicksonii* Wright. Oesterr. Botan. Zeitschr., 28: 321. [*Eurychasma dicksonii*.]
- HEWATT, W. G. AND J. D. ANDREWS
1954a. Mortalities of oysters in trays at Gloucester Point, York River, Virginia. Natl. Shellfisheries Assn. 1953 Convention Addresses, p. 78. (Abstract) [*Dermocystidium marinum* probably involved in mortality.]
1954b. Oyster mortality studies in Virginia. I. Mortalities of oysters in trays at Gloucester Point, York River. Texas Jour. Sci., 6: 121-133. [*Dermocystidium marinum*.]
1956. Temperature control experiments on the fungus disease, *Dermocystidium marinum*, of oysters. Proc. Natl. Shellfisheries Assn., 46: 129-132.
- HILEN, ETHYL J.
1923. Report on a bacteriological study of ocean slime. Rept. Bur. Construction and Repair, U. S. Navy Dept., Washington, D. C. (Mimeographed) [Unnamed molds occurring in slime.]
- HOFER, B. VON
1883. Eine Salmoidenkränkung. Allgemeine Fischerei-Zeit., (N. S.), 8: 168. (Not seen) [Parasite of trout described, not identified; (probably *Ichthyophonus Ichthyosporidium*).]
1904. Handbuch der Fischkrankheiten. 359 pp. München. [Mentions fungus similar to *Ichthyophonus hoferi*, but no name or concise description.]
1906. Handbuch der Fischkrankheiten. Stuttgart. (Same as 1904 publication.)
- HÖHNK, W.
1939. Ein Beitrag zur Kenntnis der Phycomyceten des Brackwassers. Kieler Meeresforsch., 3: 337-361. [*Pythium maritimum* n. sp., *Pythiogeton* sp., *Pythiomorpha* sp., *Saprolegnia* sp., and *Pythium monospermum* described. Distribution in relation to salinity.]
1952a. Die in Nordwestdeutschland gefundenen ufer- und bodenbewohnenden Saprolegniaceae. Veröffent. Inst. Meeresforsch., Bremerhaven, 1: 52-90. [Ecological observations; fungi from coastal beach soil; 2 n. spp. *Brevilegnia*; *Aplanopsis terrestris* n. gen., n. sp.]
1952b. Nachtrag zu: Die in Nordwestdeutschland gefundenen ufer- und bodenbewohnenden Saprolegniaceae. Veröffent. Inst. Meeresforsch.,

Bremerhaven, 1: 126-128. [Latin descriptions of fungi described in previous paper.]

- 1952c. Studien zur Brack- und Seewassermykologie I. Veröffent. Inst. Meeresfors., Bremerhaven, 1: 115-125. [Thirty-one fungi isolated from brackish water and beach soils; culture studies in relation to salinity.]
- 1952d. Studien zur Brack- und Seewassermykologie II. Oomycetes: Erster Teil. Veröffent. Inst. Meeresfors., Bremerhaven, 1: 247-278. [Pythiaceae and Saprolegniaceae from brackish water; salinity tolerance and influence of salinity on sexual and asexual reproduction.]
- 1953a. Studien zur Brack- und Seewassermykologie III. Oomycetes: Zweiter Teil. Veröffent. Inst. Meeresfors., Bremerhaven, 2: 52-108. [Twenty-nine filamentous fungi described, including 3 n. spp. and 2 n. vars. of *Pythium*; some spp. previously recorded from fresh water or terrestrial habitats reported from brackish water. Saline tolerances recorded for these fungi.]
- 1953b. Eine neue uferbewohnende Saprolegniacee: *Calyptralegnia ripariensis* nov. spec. Veröffent. Inst. Meeresfors., Bremerhaven, 2: 230-235.
- 1953c. Mykologische studien im Brack- und Seewasser. Atti del VI. Cong. Internat. Microbiol., Roma, 7: 374-378. [Summarized report on salinity tolerance studies.]
- 1954a. Studien zur Brack- und Seewassermykologie IV. Ascomyceten des Küstensandes. Veröffent. Inst. Meeresfors. Bremerhaven, 3: 27-33. [*Arenariomyces* n. gen., and *A. cinctus*, *A. trifurcatus* n. spp. (*A. cinctus* synonymous with *Peritrichospora integra* Linder, according to Johnson, 1956b; *A. trifurcatus* placed in *Halosphaeria*, Cribb & Cribb, 1956.)]
- 1954b. Von den Mikropilzen in Watt und Meer. Abhandl. Naturwiss. Vereins, Bremen, 33: 407-429. [Brief historical sketch; ecological (particularly salinity) and culture factors; drawings of an unnamed, lignicolous Ascomycete.]
- 1955a. Studien zur Brack- und Seewassermykologie V. Höhere Pilze des submersen Holzes. Veröffent. Inst. Meeresfors., Bremerhaven, 3: 199-227. [Five n. spp., and 2 n. vars. of Ascomycetes; 3 spp. (1 new) of Fungi Imperfecti; distributional data.]
- 1955b. Niedere Pilze vom Watt und Meeresgrund (Chytridiales und Thraustochytriaceae). Naturwissenschaften, 42: 348-349. [Distribution (numerical) in relation to salinity.]
- 1956a. Mykologische Abwasserstudie I. Veröffent. Inst. Meeresfors. Bremerhaven, 4: 67-110. [Not marine; author states this series of studies to be a parallel to his marine fungus investigations.]
- 1956b. Studien zur Brack- und Seewassermykologie VI. Über die pilzliche Besiedlung verschieden salziger submerser Standorte. Veröffent. Inst. Meeresfors., Bremerhaven, 4: 195-213. [Numerical distribution of filamentous Phycomycetes in relation to salinity.]

HÖHNK, W. AND A. A. ALEEM

- 1953. Ein Brackwasserpilz: *Olpidium maritimum* nov. spec. Veröffent. Inst. Meeresfors., Bremerhaven, 2: 224-229.

HÖHNK, W. AND S. VALLIN

- 1953. Epidemisches Absterben von *Eurytemora* im Bottnischen Meerbusen, verursacht durch *Leptolegnia baltica* nov. spec. Veröffent. Inst. Meeresfors., Bremerhaven, 2: 215-223.

HOOKER, J. D. AND W. H. HARVEY

1845. Algae Antarcticae: Chlorospermeae. Jour. de Bot., 4: 293-298. [*Guignardia prasiolae*, described as *Ulva tessellata*.]
1847. Flora Antarctica II. Algae. London. [The genus *Mastodia* formed to receive *Ulva tessellata* (= *Guignardia*).]

HØYE, K.

1902. Undersøgelser over klipfiskesoppen. Bergens Mus. Aarb., No. 7, 1901: 1-40. [Describes, but does not name, *Torula epizoa*; (Frank and Hess, 1941a, assume this fungus to be *Sporendonema epizoum*, causing "dun" of salt fish). Salt tolerance studies.]
1905. Undersøgelser over klipfiskesoppen. Bergens Mus. Aarb., No. 9, 1904: 1-106. [Continued study and results of salt tolerance investigation of *Torula epizoa*.]
1907. Recherches sur la moisissure de Bacalao et quelques autres micro-organismes halophiles. Bergens Mus. Aarb., No. 12, 1906: 1-64. [Halophilic molds on dry, salt codfish: *Torula epizoa*, *T. minuta* n. sp., *Sarcinomyces islandicus* n. sp., *S. niger* n. sp., *S. sporigenus* n. sp., *Hormodendrum halophilum*, 3 yeast forms, *Penicillium glaucum*, *Aspergillus glaucus*; distributional data and salt tolerance of these fungi.]
1909. Untersuchungen über die Schimmelbildung des bergfisches. Bergens Mus. Aarb., No. 14, 1908: 1-29. [Culture studies on *Torula epizoa*; methods of disinfection to destroy fungus in salt fish processing.]

HUMPHREY, J. E.

1893. The Saprolegniaceae of the United States, with notes on other species. Trans. American Phil. Soc., (N. S.), 17: 63-148. [*Achlya penetrans*, described as fungus by Duncan, 1876, is siphonaceous alga.]

HUNTER, A. C.

1920. A pink yeast causing spoilage in oysters. U. S. D. A. Bull. No. 819, pp. 1-24. [*Torula* in oyster beds and on healthy oysters.]

HUNTSMAN, A.

1933. Disease in eel-grass. Biol. Bd. Canada, Progress Reports, 1932, p. 11.

INGLE, R. M. AND C. E. DAWSON

1953. A survey of Appalachicola Bay. Tech. Ser., Florida State Bd. Conservation, Tallahassee, No. 10. [Report of *Dermocystidium marium* in oysters.]

ISSACHENKO, B. L.

1914. Investigations on the bacteria of the glacial Arctic Ocean. 300 pp. Monograph. Petrograd. (In Russian; not seen.) [Yeasts reported but not named.]

IVIMEY-COOK, W. R.

1932. The parasitic slime-moulds. Hong Kong Nat., Suppl., No. 1, pp. 29-39. [*Ostenfeldiella diplantherae* synonymous with *Plasmodiophora diplantherae*; description of *Tetramyxa parasitica* on marine and brackish water angiosperms.]
1933. A monograph of the Plasmodiophorales. Arch. Protistenk., 80: 179-254. [*Plasmodiophora diplantherae* (= *Ostenfeldiella diplantherae* of Ferdinansen & Winge, 1914).]

JACZEWSKI, A. A.

1931. Opredelitel gribov. Sovershennye griby (diploidnye stadii). (Determination of fungi. Perfect fungi, diploid species). Moskva, Leningrad,

Gosudarstvennoe izdatel'stvo sel' skokhoziaistvennoi i kolkhoznoko-operativnoi literatura. I. Fikomitsety (Phycomycetes). 294 pp. [Proposes nom. nov., *Deckenbachia* for *Coenomyces* described by Deckenbach, 1903.]

JEPPE, MARGARET W.

1931. Note on a marine *Labyrinthula*. Jour. Marine Biol. Assn., United Kingdom, (N.S.), 17: 833-838. [Described, not named.]

1937. On the protozoan parasites of *Calanus finmarchicus* in the Clyde Sea area. Quart. Jour. Micr. Sci., 79: 589-658. [*Ichthyosporidium* as a protozoan.]

JIROUEC, O.

1956. Parasiten der Rotatorien im Plankton javanischer Seen. Suppl., Arch. Hydrobiol., 23: 105-108. [*Olpidium* sp. in *Brachionus falcatus*.]

JOHNSON, R. A. AND F. A. MCNEIL

1941. Supplementary report No. 2. Maritime Services Board of New South Wales, p. 36. [Record of unidentified Ascomycete in submerged hardwood.]

JOHNSON, T.

1909. *Chrysophlyctis endobiotica* Schilb. (potato wart or black scab), and other Chytridiaceae. Sci. Proc. Royal Dublin Soc., 12: 131. [Mention of *Chytridium sphacellarum*.]

JOHNSON, T. W., JR.

1955. The genus *Achlya*: morphology and taxonomy. 180 pp. Univ. Michigan Press: Ann Arbor. [*Achlya penetrans*, a fungus in mollusc shells according to Duncan, 1876, excluded from genus; suggests fungus is an alga.]

1956a. Marine fungi. I. *Leptosphaeria* and *Pleospora*. Mycologia 48: 495-505. [Six spp. of *Leptosphaeria* described, 1 new; *Pleospora pelagica* n. sp.]

1956b. Marine fungi. II. Ascomycetes and Deuteromycetes from submerged wood. Mycologia, 48: 841-851. [Six Fungi Imperfecti and 9 Ascomycetes described. *Stemphylium maritimum*, *Massariella maritima*, and *Sphaerulina pedicellata* n. spp.; unnamed spp. in genera *Hormiscium*, *Sphaerulina*, *Physalospora*, and *Ceratospheeria*. *Arenariomyces cinctus* Höhnk synonymous with *Peritrichospora integra* Linder.]

1956c. Ascus development and spore discharge in *Leptosphaeria discors*, a marine and brackish-water fungus. Bull. Marine Sci. Gulf and Caribbean, 6: 349-358.

JOHNSTONE, J.

1905. Internal parasites and diseased conditions of fishes. Rept. for 1905, Lancashire Sea Fisheries Lab., No. 14, pp. 151-185. [Fungus in *Pleuronectes platessa*; suggests in Entomophthoraceae, near *Conidiobolus*.]

1906. Internal parasites and diseased conditions of fishes. Trans. Biol. Soc., Liverpool, 20: 179-185. [Describes but does not name a fungus suggestive of *Conidiobolus*. (Sproston, 1944, says the description agrees with *Ichthyosporidium hoferi* in mackerel.)]

1912. Diseased conditions of fishes. Rept. for 1912, Lancashire Sea Fisheries Lab., No. 21, pp. 20-42. [*Ichthyophonous hoferi* in mackerel; fungus considered a Phycomycete; etiology and symptomatology.]

1913. Diseased conditions of fishes: a phycomycetous fungus in a mackerel (*Scomber scomber*). Trans. Biol. Soc., Liverpool, 27: 28-33. [De-

scribes but does not name fungus similar to *Ichthyosporidium hoferi*.]

1920. On certain parasites, diseased and abnormal conditions of fishes. Rept. for 1919, Lancashire Sea Fisheries Lab., No. 28, pp. 24-33. [*Ichthyophonus* (= *Ichthyosporidium*) *hoferi*.]

JOKL, M.

1916. Eine neue Meereschytridinee: *Pleotrachelus ectocarp*i, nov. spec. Oesterr. Bot. Zeitschr., 66: 267-272. [(Synonymous with *Olpidiopsis andreei*, according to Sparrow.)]

JONES, H. L.

1898. A new species of Pyrenomycete parasitic on an alga. Bull. Oberlin College Lab., 9: 3. (Not seen) [*Sphaerella chondri* (= *Leptosphaeria chondri*).]

JUEL, H. O.

- 1901a. *Pyrrhosorus*, eine neue marine Pilzgattung. Bih. Kgl. Svensk Vetensk.-Ak. Handl. 26, Afd. 3, No. 14, pp. 1-16.
1901b. *Pyrrhosorus*, eine neue marine Pilzgattung. Rev. Mycologique, 23: 111-112. [*P. marinus*; same as previous publication.]

KARLING, J. S.

- 1942a. The Plasmodiophorales. Publ. by the author, New York. [Marine species of *Plasmodiophora* described; none new.]
1942b. Simple holocarpic biflagellate Phycomycetes. Publ. by the author, New York. [Descriptions and taxonomic notes on several previously described marine Phycomycetes.]
1943. The life history of *Anisopodium ectocarp*ii, gen. nov. et sp. nov., and a synopsis and classification of other fungi with anteriorly uniflagellate zoospores. Amer. Jour. Bot., 30: 637-648.

KAWAGUCHI, S.

1942. Investigation on reef-corals. 3. Kagaku Nauyo (Sci. South Sea), 5: 95-106. [Applies name *Achlya penetrans* (given to fungus in mollusc shells by Duncan, 1876) to a green alga parasitic on reef coral.]

KIBBE, ALICE L.

1915. Some points in the structure of *Alaria fistulosa*. Publ. Puget Sound Biol. Sta., 1: 43-57. [Describes "papillate" bodies on sporophyll surfaces of *A. fistulosa*, which, in 1916 paper, says appear to be due to fungus sporangia (presumably of *Chytridium alarium*).]
1916. *Chytridium alarium* on *Alaria fistulosa*. Publ. Puget Sound Biol. Sta., 1: 221-226. [(Alga cystidia described as marine fungus.)]

KNOYLE, J. MARY

1952. The life history and biology of *Leptosphaeria chondri* (Rostr.) Rosenv. Master's Thesis, University of Wales, Aberystwyth. [Includes description of pycnidia; suggests fungus is not a leptosphaeria because of spore septation pattern.]

KNY, L.

1871. *Chytridium* (*Olpidium*) *sphacellarum*. Sitzungsber. Gesell. Naturforsch. Freunde zu Berlin, 1871: 93-97. (Also in Hedwigia, 11: 81-87. 1872.)

KOBAYASHI, Y.

1953. Outline of the investigations about marine fungi. Nagaoa, 3: 123-129. [Summary of Japanese studies on marine Phycomycetes.]

KOBAYASHI, Y. AND M. OOKUBO

1953. Studies on the marine Phycomycetes. Bull. Nat. Sci. Museum, Tokyo.

33: 53-65. [Describes 4 n. spp., 3 n. vars., and n. gen. *Japonochytrium*.]

1954. Studies on the marine Phycomycetes. II. Bull. Nat. Sci. Museum, Tokyo, (N.S.), 1: 62-71. [Six n. spp., 2 n. vars., and an unnamed species of *Eurychasma*.]

KÖLLIKER, A.

- 1859-60. On the frequent occurrence of vegetable parasites in the hard structure of animals. Proc. Royal Soc. London, 10: 95-99. [Shell-boring "fungi".]

1860a. Über das ausgebreitete Vorkommen von Pflanzen Parasiten in den Hartgebilden niederer Thiere. Zeitschr. wiss. Zool., 10: 215-232. [Shell-boring "fungi".]

- 1860b. On the frequent occurrence of vegetable parasites in the hard tissues of the lower animals. Quart. Jour. Micr. Sci., 8: 171-187. [Shell-boring "fungi".]

KORRINGA, P.

1948. Shell disease in *Ostrea edulis*, its dangers, its cause, its control. Convention Addresses, Natl. Shellfisheries Assn., 1948. [Shell-boring fungus described, not named.]

LAGERHEIM, G.

1899. Om växt-och djurlämningarna i Andrées polarboj. In Ymer, Tidsskr. Svenska Sällskap. Antropol. Geogr., 19: 425-433. [Report of *Pleotrachelus (Olpidiopsis) andreei*.]

LANGHORNE, W. H.

1953. The effect of temperature on the development of *Dermocystidium marinum*. Rept., Biol. Dept., Univ. of the South, Sewanee, Tennessee. (Manuscript).

LAVERAN, A. AND A. PETTIT

1910. Sur une épizootie des truites. Comptes Rendus Acad. Sci., Paris, 151: 421-423. [Describes protozoan. (Description suggests fungus parasite.)]

LAVIER, G.

1938. Sur un protophyte parasite intestinal de poisson marin. Ann. Parasitol., 16: 259-264. [An achlorophyllous, Oscillatoria-like organism, *Anacamptothrix intestinalis*, in a marine fish. (Probably not fungoid, although figures and description suggest an eccrinid.)]

LÉGER, L.

1927. Sur la nature et l'évolution des "sphérules" décrites chez les Ichthyophones, Phycomycètes parasites de la Truite. Comptes Rendus Acad. Sci., Paris, 180: 1268-1271. [Revision of taxonomic status of *I. hoferi*.]

1929. Sur la nature et l'évolution des sphérules décrites chez les *Ichthyophonus* Phycomycètes parasite de la truite. Ann. Univ. Grenoble Sci. Med., (N.S.), 6: 133-137. [Places *Ichthyosporidium hoferi* in genus *Ichthyophonus*, in Phycomycetes.]

LEMMERMANN, E.

1901. Die parasitischen und saprophytischen Pilze der Algen. Abhandl. Naturwiss. Ver., Bremen, 17: 185-202. [Mention of *Dothidella laminariae*.]

LENDENFELD, R. V.

1889. A monograph of the horny sponges. 936 pp. Publ. by the Royal So-

ciety, London. [Fungus-like filaments are considered to be horn-like precipitations.]

LIEBERKÜHN, N.

1859. Neue Beiträge zur Anatomie der Spongien. Archiv Anat. Physiol. Wissensch. Medizin, pp. 353-382, 515-529. [Illustrates and mentions fungus filaments in sponges.]

LIND, J.

1905. Ueber einige neue und bekannte Pilze. Ann. Mycol., 3: 427-432. [*Rhizophyidium gelatinosum*. (Doubtful if fungus, Sparrow, 1943.)]
1931. Danish fungi as represented in the herbarium of E. Rostrup. Copenhagen. [*Leptosphaeria chondri*.]

LLOYD, B.

1947. Marine fungi. Thesis, Univ. College of Wales, Aberystwyth. (Not seen)

LLOYD, L. S.

1956. The life history of *Lulworthia medusa* (Ellis and Everhart) Cribb and Cribb. Master's Thesis, Univ. of Wales, Aberystwyth. [In addition to detailed developmental cycle, describes *L. lanosa* n. sp., and gives brief discussion of the position of the genus *Lulworthia*.]

LÖWENTHAL, W.

1904. Weitere Untersuchungen an Chytridiaceen. II. *Olpidium Dicksonii* (Wright) Wille. Arch. Protistenk., 5: 221-239.

LUND, A.

1930. A new species of *Pleotrachelus* with remarks on this genus. Bot. Tidsskr., 41: 240-243.

LUTHER, H.

1950. Beobachtungen über *Tetramyxa parasitica* Goebel. Mem. Soc. pro Fauna et Flora Fennica, 25: 88-96. (1948-49) [New records of plasmodiophoraceous parasites.]

MACKIN, J. G.

1951. Histopathology of infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum* Mackin, Owen, and Collier. Bull. Marine Sci. Gulf and Caribbean, 1: 72-87. [(See for other references to oyster diseases, which may or may not be caused by *D. marinum*.)]
1952a. Fifth *Dermocystidium* infection experiment. Tech. Rept. 2, Texas A. & M. Res. Foundation. 5 pp.
1952b. A study of transmission of infective elements of *Dermocystidium marinum* by way of water currents. Tech. Rept. 3, Texas A. & M. Res. Foundation. 6 pp.
1953a. A study of the effect of infection by *Dermocystidium* on ciliary action in oysters. Tech. Rept. 8, Texas A. & M. Res. Foundation. 5 pp.
1953b. Summary of the results of thioglycollate culture diagnoses of *Dermocystidium* disease in oysters made at the Grand Isle Laboratory of the Texas A. & M. Research Foundation. Tech. Rept. 9, Texas A. & M. Res. Foundation. 5 pp.
1953c. Incidence of infection of oysters by *Dermocystidium* in the Barataria Bay area of Louisiana. Natl. Shellfisheries Assn. 1951 Convention Addresses, pp. 22-35.
1954a. Records of the distribution of *Dermocystidium marinum* in Louisiana with data on the incidence of infection of oysters. Tech. Rept. 16, Texas A. & M. Res. Foundation. 6 pp.

- 1954b. Resistance of populations of oysters with high weighted incidence of *Dermocystidium marinum* to holding out of water. Tech. Rept. 18, Texas A. & M. Res. Foundation. 6 pp.
1956. *Dermocystidium marinum* and salinity. Proc. Natl. Shellfisheries Assn., 46: 116-128.
- MACKIN, J. G. AND J. L. BOSWELL
1953. A study of the effect of salinity variation on *Dermocystidium* infection in oysters. Tech. Rept. 5, Texas A. & M. Res. Foundation. 12 pp.
1956. The life cycle and relationships of *Dermocystidium marinum*. Proc. Natl. Shellfisheries Assn., 46: 112-115.
- MACKIN, J. G. AND F. CAUTHRON
1954. Additional studies of the effect of infection by *Dermocystidium* on ciliary action in oysters. Tech. Rept. 12, Texas A. & M. Res. Foundation. 8 pp.
- MACKIN, J. G., H. M. OWEN AND A. COLLIER
1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum* n. sp., in *Crassostrea virginica* (Gmelin). Science, (N.S.), 111: 328-329.
- MACKIN, J. G. AND S. M. RAY
1954. Studies on the effect of infection by *Dermocystidium marinum* on ciliary action in oysters (*Crassostrea virginica*). Proc. Natl. Shellfisheries Assn., 45: 168-181. (Also in 1954 Convention Addresses.)
- MAGNUS, P.
1872. . . . Ueber ein *Chytridium* . . . Sitzungsber. Gesell. Naturforsch. Freunde zu Berlin, 1872: 87-90. [*Chytridium tumefaciens* (*Eurychasmodium*).]
1875. Die botanischen Ergebnisse der Nordseefahrt vom 21. Juli bis 9. September 1872. In Jahresber. der Commission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel für die Jahre 1872, 1873, 2-3: 59-80. [Chapter 3 - describes and reports *Chytridium tumefaciens*, *C. sphacellarum*, *C. plumulae*. (See Sparrow, 1943, for taxonomic status of these spp.)]
1905. Über die Gattung, zu der *Rhizophydium Dicksonii* Wright gehört. Hedwigia, 44: 347-349. [Places species in *Eurychasma* n. gen.]
- MAIRE, R. AND E. CHEMIN
1922. Un nouveaux Pyrénomycète marin. Comptes Rendus Acad. Sci., Paris, 175: 319-321. [*Mycaureola dilseae*.]
- MAIRE, R. AND A. TISON
1911. Nouvelles recherches sur les Plasmodiophoracées. Ann. Mycol., 9: 226-246. [Reports *Tetramyxa parasitica* in *Ruppia rostellata*, *Zanichellia polycarpa*, and *Z. palustris*.]
- MARTIN, G. W.
1922. *Rhizophydium polysiphoniae* in the United States. Bot. Gaz., 73: 236-238.
- MASSEE, G.
1892-93. Bibliography (edited by Masee). Grevillea, 21: 23-28. [On p. 26, reviews paper by Bornet, 1881.]
- MATTICK, F.
1953. Lichenologische Notizen. 4. Gedanken zur Phylogenie der Flechten. Ber. Deutsch. Bot. Gesell., 66: 271-275. [*Mycosphaerella pelvetiae*

on *Pelvetia canaliculata* as a case of parasitism becoming an established symbiosis.]

MENZEL, R. W. AND S. H. HOPKINS

1954. Effects of two parasites on the growth of oysters. Proc. Natl. Shellfisheries Assn., 45: 184-186. (Also in 1954 Convention Addresses.) [*Dermocystidium marinum*.]

MEYERS, S. P.

1953. Marine fungi in Biscayne Bay, Florida. Bull. Marine Sci. Gulf and Caribbean, 2: 590-601. [Two forms of Pyrenomycetes, and 4 dissimilar groups of *Halophiobolus* (*Lulworthia*) described.]
1954. Marine fungi in Biscayne Bay, Florida. II. Further studies of occurrence and distribution. Bull. Marine Sci., Gulf and Caribbean, 3: 307-327. [Five forms of Pyrenomycetes described; culture studies reported. (See subsequent papers for nomenclature.)]
1956. Taxonomy of marine Pyrenomycetes. Doctoral Dissertation: Columbia Univ., New York. [Two n. gen., 5 n. spp., and 1 n. var.; *Dothiella pelvetiae*, *Endodothella laminariae*, *Pharcidia marina*, and *Othiella cystophorae* transferred to other genera; keys to genera and some spp.; host index; 6 spp. 1 genus reduced to synonymy; 1 var. raised to specific rank. Culture studies and variations in ascocarps.]

MINDEN, M. VON

1915. Chytridiineae. Kryptogamen-Fl., Mark Brandenburg, 5(2): 193-352. (1911) [Compilation of species, some marine.]

MIYABE, K. AND J. TOKIDA

1948. Black-dots disease of *Gloiopeltis furcata* Post. et Rupr. caused by a new ascomycetous fungus. Bot. Mag., Tokyo, 61: 116-118. [*Guignardia gloiopeltidis*. (Preliminary report by J. Tokida, in Jour. Hokkaido Fish. Sci. Inst., vol. 5; in Japanese; not seen.)]

MONTAGNE, J. F. C.

1856. Sylloge generum specierumque Cryptogamarum. Paris. [*Sphaeria posidoniae*.]

MOORE, R. T.

1955. Index to the Helicosporae. Mycologia, 47: 90-103. [Includes key to marine spp. of *Helicoma*.]

MOUNCE, IRENE

1934. Disease in eel-grass. Biol. Bd. Canada, Progress Reports, 1933, p. 26. [Fungus associated with wasting disease.]

MOUNCE, IRENE AND W. W. DIEHL

1934. A new *Ophiobolus* on eelgrass. Can. Jour. Res., 11: 242-246. [*Ophiobolus halimus* (*Lulworthia* and *Halophiobolus*, later generic names).]

MÜLLER, E.

1950. Die schweizerischen Arten der Gattung *Leptosphaeria* und ihrer Verwandten. Sydowia, 4: 185-319. [Includes descriptions of some marine or brackish water leptosphaerias.]

MULSOW, K.

1911. Die Taumelkrankheit der Salmoniden. Allgemeine Fischerei-Zeit., 35: 146-148.

NADSON, G. AND G. BURWITZ

1931. Hefer des Nördlichen Eismeer. Comptes Rendus Acad. Sci., URSS, pp. 103-110. (Not seen) [Yeasts isolated from marine algae; also *Dematiium*, *Oidium*, and *Endomyces*.]

NEEDLER, A. W. H. AND R. R. LOGIE

1947. Serious mortalities in Prince Edward Island oysters caused by a contagious disease. Trans. Royal Soc., Canada, Ser. 3, Sect. 5, 41: 73-89. [Cause not determined; suggest sporozoan parasite (description suggests fungus agent).]

NERESHEIMER, E. AND C. CLODI

1914. *Ichthyophonus hoferi* Plehn und Mulsow, der Erreger der Taumelkrankheit der Salmoniden. Arch. Protistenk., 34: 217-248.

NIEZABITOWSKI, E. L.

1913. Pasorzyty roślinne morkich raków glebinowych z rodzaju *Pasiphaea*. (Die pflanzlichen Parasiten der Tiefsee-Decapoden-Gattung *Pasiphaea*). Kosmos, 38: 1563-1572. [Thalassomycetinae n. fam., *Thalassomyces* n. gen., *T. spiczakovii* and *T. batei* n. spp.; family placed in Oomycetes. (Figures of these two spp. are more suggestive of one of the Fungi Imperfecti.)]

OLLIVIER, G.

1926. *Thalassoascus Tregoubovii* (nov. gen., nov. sp.), Pyrénomycète marin parasite des Cutlériacées. Comptes Rendus Acad. Sci., Paris, 182: 1348. [(See Feldmann, 1932.)]
1928. Contribution à la connaissance de la flore marine des Alpes-Maritimes. Bull. l'Inst. Océanogr., Monaco, paper 522, pp. 1-8. [Mention of *Thalassoascus (Melanopsamma) tregoubovii* on *Cystoseira*; *Amphisphaeria biturbinata* on *Posidonia*; *Eurychasma dicksonii*. Reports finding "pycnidial" forms similar to those described by Rolland, 1896.]
1929. Étude de la flore marine de la Côte d'Azur. Ann. Inst. Océanogr., (N.S.), 7: 53-173. (1930) [Chapter 6, pp. 165-173, marine Pyrenomycetes. Describes *Melanopsamma tregoubovii* n. sp., *M. tregoubovii* var. *cutleriae* n. var. (*Thalassoascus tregoubovii*, synonym), *M. tregoubovii* var. *cystoseirae*; reports *Amphisphaeria posidoniae*.]

OSTENFELD, C. H. AND H. E. PETERSEN

1930. On a new Plasmodiophoracea found in Canada. Zeitschr. Bot., 23: 13-18. [Cite *Thecaphora ruppiae* on *Ruppia maritima* var. *rostrata* as synonymous with *Tetramyxa parasitica*.]

OSTENFELD-HANSEN, C.

1897. Contribution à la flore de l'île Jan-Mayen. Bot. Tidsskr., 21: 18-32. [In part D, Champignons, by E. Rostrup, lists *Dothidella laminariae* on *Laminaria agardhii*.]

OUDEMANS, C. A. J. A.

1894. Over twee nog onbekende fungi: *Septoria Dictyotae* en *Ustilago Vuyckii*. Verslag Zittingen wis- en natuurkundige Afd., Koninklijke Akad. van Wetensch., 3: 54-57. (1895) [*Septoria* on *Dictyota obtusangula*.]

PAPENFUSS, G. F.

1935. Alternation of generations in *Ectocarpus siliculosus*. Bot. Gaz., 96: 421-446. [Mention of an unnamed chytrid parasite.]

PATOUILLARD, N.

1897. *Zignoella calospora*. Jour. de Bot., 11: 242.

PATOUILLARD, N. AND P. HARIOT

1903. Une algue parasitée par une Sphériacée. Jour. de Bot., 17: 228. [*Zignoella enormis* on *Stypocaulon scoparium*.]

PETERSEN, H. E.

1905. Contributions à la connaissance des Phycomycètes marins (Chytridiaceae Fischer). Oversigt. Kgl. Danske Vidensk. Selskabs. Forhandl., 1905: 439-488. [First comprehensive study of marine Phycomycetes; describes fungi in genera now known as *Petersenia*, *Sirolopidium*, *Olpidium*, *Ectrogella*, *Rhizophydium*, *Pleotrachelus*, and *Pontisma*. (See Sparrow, 1943, for discussions of Petersen's spp.)]
1933. Wasting disease of eel-grass. Nature, 132: 1004. [Ophiobolus-like fungus associated with the disease.]
1935. Preliminary report on the disease of eel-grass (*Zostera marina* L.) Rept. Danish Biol. Sta., 40: 1-8.
1936. Studies on a parasitic fungus in the Eelgrass, *Zostera marina* L. Bot. Tidsskr., 43: 1-9. [Ophiobolus-like fungus causing wasting disease.]

PETRAK, F.

1952. Über die Gattungen *Gaeumannomyces* V. Arx et Olivier, *Halophiobolus* Linder und *Linocarpon* Syd. Sydowia, 6: 383-388. [Suggests that *Halophiobolus maritimus*, *H. medusa*, and *H. halimus* are members of the genus *Linocarpon*, as is, possibly, *H. salinus*. Contends that long-necked spp. of *Halophiobolus* cannot be distinguished from genus *Ophioceras*.]

PETTIT, A.

1911. A propos du microorganisme producteur de la Taumelkrankheit: *Ichthyosporidium* ou *Ichthyophonus*. Comptes Rendus, Séances et Mém. Soc. Biol., Paris, 70: 1045-1047.
1913. Observations sur l'*Ichthyosporidium* et sur la maladie qu'il provoque chez la truite. Ann. Inst. Pasteur, 27: 986-1008. [Changes *Ichthyophonus hoferi* to genus *Ichthyosporidium*.]

PHAFF, H. J., E. M. MRAK AND O. B. WILLIAMS

1952. Yeasts isolated from shrimp. Mycologia 44: 431-451. [Eleven previously described spp., 5 n. spp., and one n. var.; temperature and salt tolerance studies.]

PICARD, F.

1908. Sur une Laboulbéniaçée marine (*Laboulbenia marina* n. sp.) parasite d'*Aepus Robini* Laboulbène. Comptes Rendus, Séances et Mém. Soc. Biol., Paris, 65: 484-486.
1913. Contribution à l'étude des Laboulbéniaçées d'Europe et du Nord de l'Afrique. Bull. Soc. Myc., France, 29: 503-571. [*Laboulbenia marina*, on a marine Carabidae.]

PLEHN, M. AND M. MULSOW

1911. Der Erreger der "Taumelkrankheit" der Salmoniden. Centralbl. Bakt. Parasitenk., 59: 63-68. [*Ichthyophonus hoferi*.]

POISSON, R.

1929. Recherches sur quelques Eccrinides parasites de Crustacés, Amphipodes et Isopodes. Arch. Zool. Exp. Gén., 69: 179-216. [Discussion of affinities of Eccrinales bearing on marine representatives.]

POLÉJAEFF, N.

1884. Report on the Keratosa collected by H. M. S. Challenger during the years 1873-1876. Challenger Reports, Zool., 11: 1-88. [Reviews, pp. 12-16, controversies concerning fungus-like filaments in sponges. Describes and illustrates filaments.]

PROKOP, J. F.

1950. Infection and culture procedures employed in the study of *Dermocystidium marinum*. Rept., Texas A. & M. Research Foundation. (Mimeographed).

RABENHORST, L.

1868. *Flora Europaea Algarum* . . . Vol. 3, 461 pp. Leipzig, 1864-68. [*Phlyctidium plumulae*.]

RATTRAY, J.

1887. Note on *Ectocarpus*. Trans. Royal Soc., Edinburgh, 32: 589-600. (1885) [Report of *Eurychasma dicksonii*.]

RAY, S. M.

- 1952a. A culture technique for the diagnosis of infection with *Dermocystidium marinum* Mackin, Owen, and Collier in oysters. Science, (N.S.), 116: 360-361.
 1952b. Cultural studies of *Dermocystidium marinum* with special reference to diagnosis of this parasite in oysters. Master's Thesis, Rice Institute.
 1952c. A culture technique for the diagnosis of infection with *Dermocystidium marinum* in oysters. Natl. Shellfisheries Assn. 1952 Convention Addresses, pp. 9-13.
 1954a. Biological studies of *Dermocystidium marinum*, a fungus parasite of oysters. Rice Institute Pamphlet, Special Issue, Nov. 1954, pp. 1-114.
 1954b. Experimental studies on the transmission and pathogenicity of *Dermocystidium marinum*, a fungous parasite of oysters. Jour. Parasit., 40: 235.
 1954c. Studies on the occurrence of *Dermocystidium marinum* in young oysters. Natl. Shellfisheries Assn. 1953 Convention Addresses, pp. 80-92.

RAY, S. M. AND A. C. CHANDLER

1944. *Dermocystidium marinum*, a parasite of oysters. Exp. Parasitol., 4: 172-200.

RAY, S. M. AND J. G. MACKIN

1954. Studies of pathogenesis of *Dermocystidium marinum*. Proc. Natl. Shellfisheries Assn., 45: 164-167.

RAY, S. M., J. G. MACKIN AND J. L. BOSWELL

1953. Quantitative measurement of the effect on oysters of disease caused by *Dermocystidium marinum*. Bull. Marine Sci. Gulf and Caribbean, 3: 6-24. [(Includes, as addendum, statistical computations by R. O. Reid, 1953.)]

REED, MINNIE

1902. Two new ascomycetous fungi parasitic on marine algae. Univ. California Publ. Bot., 1: 141-164. [*Guignardia alaskana* and *G. ulvae*. (See Cribb & Cribb, 1956, for discussion of taxonomic position of marine spp. of *Guignardia*.)]

REHM, H.

1896. Ascomycetes exsiccati fasc. 24. 1896. Hedwigia, 35: 145-151. [*Pleospora maritima*.]

REICHENBACH-KLINKE, H.-H.

- 1954a. Pilze in Tumoren bei Fischen. Verhandl. Deutsch. Zool. Gesellsch. in Tübingen, 1954, pp. 351-357.
 1954b. Untersuchungen über die bei Fischen durch Parasiten hervorgeru-

fenen Zysten und deren Wirkung auf den Wirtskörper. I. Zeit. Fischerei Hilfswissensch., (N.S.), 3: 565-636.

1955. Untersuchungen über die bei Fischen durch Parasiten hervorgerufenen Zysten und deren Wirkung auf den Wirtskörper. II. Zeit. Fischerei Hilfswissensch., (N.S.), 4: 1-54.

1956a. Die Vermehrungsformen des zoophagen Pilzes *Ichthyosporidium hoferi* (Plehn et Mulsow) (Fungi, Phycomycetes) im Wirt. Veröffent. Inst. Meeresfors., Bremerhaven, 4: 214-219.

1956b. Ueber einige bisher unbekannte Hyphomyceten bei verschiedenen Süßwasser- und Meeresfischen. Mycopath. Mycol. Appl., 7: 333-347. [Four fungi from fresh water and salt water fish; two similar to *Cladosporium*, one to the verticillias, one to *Alternaria*.]

1956c. Verbreitung und Bekämpfung des Pilzes *Ichthyosporidium hoferi* (Plehn et Mulsow) (= *Ichthyophonous hoferi*). Aquarien- und Terrarien-Zeit., 9: 70-72.

1957. Augenschäden bei Meeresfischen durch den Pilz *Ichthyosporidium hoferi* (Plehn et Mulsow) und Bemerkungen zu seiner Verbreitung bei Mittelmeeresfischen. Publ. Stat. Zool., Napoli, 29: 22-32.

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RENN, C. E.

1934. Wasting disease of *Zostera* in American waters. Nature, 134: 416. [Illustrates labyrinthula-like organism.]

1935a. A mycetozoan parasite of *Zostera marina*. Nature, 135: 544-545.

1935b. The wasting disease of eel-grass. Doctoral Dissertation, Rutgers University.

1936a. The wasting disease of *Zostera marina*. I. A phytological investigation of the diseased plant. Biol. Bull., 70: 148-158. [Casual organism is *Labyrinthula*; reviews earlier literature referring to cause as bacterial in origin.]

1936b. Persistence of the eel-grass disease and parasite on the American Atlantic Coast. Nature, 138: 507-508.

1937. The eel-grass situation along the Middle Atlantic Coast. Ecology, 18: 323-325. [Distribution of the disease with which *Labyrinthula* is associated.]

RIDDELL, W. AND D. M. ALEXANDER

1911a. Note on an ulcerative disease of the plaice. Rept. 1911, Lancashire Sea Fisheries Lab., No. 20, pp. 85-91. [Report epidemic; no traces of fungus infection.]

1911b. Note on an ulcerative disease of the plaice. Proc. Trans. Liverpool Biol. Soc., 26: 155-161. [Disease is of bacterial origin, and that similar disease described by Johnstone (1905, 1906) and attributed to fungus, is not fungal; suggests fungus described by Johnstone is secondary invader.]

RITCHIE, D. D.

1954. A fungus flora of the sea. Science, (N.S.), 120: 578-579. [Reports culture of members of genera *Aspergillus*, *Tritirachium*, *Pestalotiopsis*, *Fusarium*, *Scopulariopsis*, *Phoma*, *Gonatorhodum*, *Mucor*, and some other forms of unknown affinities, from Limon and Panama Bays, Panama, C. Z.]

ROBERTSON, M.

1908. Notes upon a Haplosporidian belonging to the genus *Ichthyosporidium*. Proc. Royal Physiol. Soc., Edinburgh, 17: 175-187. [*Ichthyosporidium* as a protozoan.]
1909. Notes on an Ichthyosporidian causing a fatal disease in sea-trout. Proc. Zool. Soc., London, 1909: 399-402. [(A protozoan, the name for which is used by other investigators for fungus infection.)]

ROGERS-TALBERT, R.

1948. The fungus *Lagenidium callinectes* Couch (1942) on eggs of the blue crab in Chesapeake Bay. Biol. Bull., 95: 214-228.

ROLLAND, L.

1896. Aliquot fungi novi vel critici Galliae. Bull. Soc. Myc., France, 12: 1-10. [Two pycnidial forms, *Sirococcus posidoniae* and *Aposphaeria boudieri*, on *Posidonia*.]

ROSENVINGE, L. K.

1906. Meddelte derefter nogle mykologiske Smaating. II. Meddelelser fra den Botaniske Forening i Kobenhavn. Bot. Tidsskr. 27: XXXIII-XXXV. [*Leptosphaeria marina* under the new name *L. chondri*.]

ROSTRUP, E.

1899. Mykologiske Meddelelser. Bot. Tidsskr., 17: 228-237. [*Leptosphaeria marina*.]
- 1894-95a. Mykologiske Meddelelser. Bot. Tidsskr. 19: 201-214. [*Dothidella laminariae* n. sp.]
- 1894-95b. Contributions mycologiques (V). Bot. Tidsskr., 19: 215-218. [Summary of previous paper.]

SACCARDO, P. A.

1879. Fungi novi ex herbario Professoris Doct. P. Magnus Berolinensis. Michelia, 1: 117-132. [Describes *Rhaphidophora maritima*, in *Zostera marina*. (Transferred to *Ophiobolus*; later, by Linder, to *Halophiobolus*, and to *Lulworthia*, by Cribb and Cribb.)]
1882. Sylloge fungorum...1: 1-768.¹
1883. Sylloge fungorum...2: 1-959.
1891. Sylloge fungorum...9: 1-1141.
1892. Sylloge fungorum...10: 1-964.
1895. Sylloge fungorum...11: 1-753.
1899. Sylloge fungorum...14: 1-1316.
1902. Sylloge fungorum...16: 1-1291.
1905. Sylloge fungorum...17: 1-991.
1912. Sylloge fungorum...21: 1-928.
1913. Sylloge fungorum...22: 1-612.
1926. Sylloge fungorum...24 (Sect. I): 1-703.
1928. Sylloge fungorum...24 (Sect. II): 704-1438.
1931. Sylloge fungorum...25: 1-1093.

SANDHOLZER, L. A., T. NOSTRAND AND L. YOUNG

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SANDOZ, M. D., M. R. ROGERS AND C. L. NEWCOMBE

1944. Fungus infection of eggs of the blue crab *Callinectes sapidus* Rathbun. Science, (N.S.), 99: 124-125.

¹Citations (in Sylloge fungorum) in which descriptions of marine and brackish water fungi appear. For names of spp. in each volume, see indices.

SANTESSON, R.

1939. Amphibious Pyrenolichens I. Arkiv för Bot., 29A: 1-67. [*Didymella conchae* Bonar (1936) is the marine lichen *Arthopyrenia sublitoralis* (Leight) Arn.]

SCATTERGOOD, L. W.

1948. A report on the appearance of the fungus *Ichthyosporidium* in the herring of the northwestern Atlantic. Spec. Report 58, U. S. Dept. Interior.

SCHAEPERCLAUS, W.

1953. Fortpflanzung und Systematik von *Ichthyophonus*. Aquarien- und Terrarien-Zeit., 6: 177-182. [*Ichthyosporidium hoferi* mentioned.]

SCHERFFEL, A.

1925. Endophytische Phycomyceten-Parasiten der Bacillariaceen und einige neue Monadinen. Ein Beitrag zur Phylogenie der Oomyceten (Schröter). Arch. Protistenk., 52: 1-141. [*Olpidium lauderiae* (*Ectrogella*); *Ectrogella licmophorae*, *E. dicksonii* (*Eurychasma*).]

SCHMIDT, O.

1862. Die Spongien des adriatischen Meeres. 88 pp. Leipzig. [Illustrates and mentions fungus filaments in certain sponges.]

SETCHELL, W. A.

1924. Three new fungi. Mycologia, 16: 240-244. [*Thecaphora ruppieae* n. sp. (Synonymous with *Tetramyxa parasitica*, Ostefeld & Petersen, 1930.)]
1926. Phytogeographical notes on Tahiti. II. Marine vegetation. Univ. California Publ. Bot., 12: 291-324. [Fungus similar to *Blodgettia confervoides* (= *B. borneti*) associated with *Cladophora fuliginosa*.]

SEYMOUR, A. B.

1929. Host index of the fungi of North America. 732 pp. Harvard Univ. Press: Cambridge. [Lists various marine Pyrenomycetes on marine algae.]

SMITH, A. L. AND J. RAMSBOTTOM

1915. Is *Pelvetia canaliculata* a lichen? New Phytol., 14: 295-298. [Discussion of *Pelvetia-Mycosphaerella*; *P. canaliculata* as infected by, or having an association with, *M. pelvetiae*, described by Sutherland, 1915a.]

SMITH, F. G. W.

1939. Sponge mortality at British Honduras. Nature, 144: 785. [Fungus filaments in diseased sponge tissue.]

SNOW, J. E. AND P. J. BEARD

1939. Bacterial flora of North Pacific salmon. Food Research, 4: 563-585. [Yeasts from salmon.]

SOROKIN, N. W.

1874. Aperçu systématique du groupe des Siphomycètes. Bull. Soc. Nat., Kazan, 4: 1-26. [*Haplocystis mirabilis* n. gen., n. sp., on submerged wood. (An imperfectly known genus of Chytridiaceae, Sparrow, 1943.)]

SPARROW, F. K., JR.

1934. Observations on marine Phycomycetes collected in Denmark. Dansk Bot. Arkiv, 8: 1-24. [New gen., *Petersenia*; 2 n. spp., 1 comb. nov.; 8 previously known spp. reported. Three spp. unnamed but described.]
1936. Biological observations on the marine fungi of Woods Hole waters.

Biol. Bull., 70: 236-263. [Fifteen spp. of Phycomycetes, 2 Myxomycetes, and a *Protomyxa*-like organism; *Eurychasmidium*, *Thraus-tochytrium*, n. gen.]

1937. The occurrence of saprophytic fungi in marine muds. Biol. Bull., 73: 242-248.

1943. Aquatic Phycomycetes, exclusive of the Saprolegniaceae and *Pythium*. Univ. Michigan Press: Ann Arbor. [Descriptions of known marine Phycomycetes, together with distributional notes and discussions.]

SPROSTON, NORA G.

1944. *Ichthyosporidium hoferi* (Plehn & Mulsow, 1911), an internal fungoid parasite of the mackerel. Jour. Marine Biol. Assn., United Kingdom, 26: 72-98. [Summary of work done on this organism to date. Detailed description of fungus, developmental history, and pathological condition induced. Contends correct nomenclature to be *Ichthyosporidium hoferi* (Plehn & Mulsow) Pettit, and provisionally places various forms previously described as fungal or protozoan parasites (under this name, or *Ichthyophonus*) in this species, or at least con-specific with *I. hoferi*.]

STEIN, J. E. AND J. G. MACKIN

1955. A study of the nature of pigment cells of oysters and the relation of their numbers to the fungus disease caused by *Dermocystidium marinum*. Texas Jour. Sci., 7: 422-429.

STIRRUP, M.

1872. On shells of mollusca showing so-called fungoid growths. Proc. Lit. Phil. Soc., Manchester, 11: 137-138. [Reports tubular structures in certain mollusc shells are due to a parasitic fungus; sporangia and sparingly branched filamentous processes on inner shell layers.]

STOLL, K.

1936. Saprolegniineen aus der Umgebung von Greifswald. Mitt. Naturwiss. Verein Neuorpommern und Rügen in Greifswald, 63-64: 20-42. [Reports occurrence of fresh water spp. *Achlya polyandra*, *A. racemosa*, *Saprolegnia dioica*, *S. thureti*, *Aphanomyces laevis*, and *Pythium proliferum*, in brackish water.]

SUTHERLAND, G. K.

1915a. New marine fungi on *Pelvetia*. New Phytol., 14: 33-43. [Four n. spp. Ascomycetes, 1 n. sp. *Macrosporium*.]

1915b. New marine Pyrenomycetes. Trans. British Myc. Soc., 5: 147-155. [Five n. spp.; 2 n. gen., *Trailia* and *Orcadia*.]

1915c. Additional notes on marine Pyrenomycetes. New Phytol., 14: 183-193. [Four n. spp.]

1916a. Marine Fungi Imperfecti. New Phytol., 15: 35-48. [Nine n. spp., in genera *Cladosporium*, *Diplodina*, *Fusidium*, *Monosporium*, *Sporotrichum*, *Cercospora*, *Macrosporium*, *Alternaria*, and *Epicoccum*.]

1916b. Additional notes on marine Pyrenomycetes. Trans. British Myc. Soc., 5: 257-263. [Three n. spp., one undescribed member of *Orcadia*; *Lulworthia* n. gen.]

TAKAMATSU, M.

1943. The species of *Sphacelaria* from Japan. I. Jour. Sigen. Ken., 1: 153-187. (Not seen) [Describes *Sphacelaria apicalis*. (The figures and description are, according to Tokida, 1948, very similar to inflated apical segments caused by a chytrid parasite, possibly *Olpidium spha-*

cellarum. If *O. sphacellarum*, placed in genus *Olpidiopsis* by Sparrow, 1943.)]

THEISSEN, F. AND H. SYDOW

1915. Die Dothideales. Ann. Mycol., 13: 149-746. [*Endodothella laminariae*.]

1918. Vorentwürfe zu den Pseudosphaeriales. Ann. Mycol., 16: 1-34. [*Endodothella laminariae* (Rostrup) Theissen & Sydow.]

TOKIDA, J.

1948. Swollen-head disease of *Sphacelaria* and swollen-foot disease of *Spongomorpha*. Bot. Mag., Tokyo, 61: 113-116. [Report of *Olpidium sphacellarum* on *Sphacelaria subfusca*, and *Olpidium* sp. on *Spongomorpha duriuscula*.]

TOKUNAGA, Y.

1933. Studies on the aquatic chytrids of Japan II. Olpidiaceae. Trans. Sapporo Nat. Hist. Soc., 13: 78-84. [*Olpidium aggregatum* on a marine *Cladophora*.]

TROTTER, A.

1904. Notulae mycologicae. Ann. Mycol., 2: 533-538. [*Ascochyta salicorniae*, on *Salicornia patula* in a "salt lake".]

TUTIN, T. G.

1934. The fungus on *Zostera marina*. Nature, 134: 573. [*Ophiobolus halimus* as probable cause of the wasting disease.]

1938. The autecology of *Zostera marina* in relation to its wasting disease. New Phytol., 37: 50-71.

VAISEY, E. B.

1954. Osmophilism of *Sporendonema epizoum*. Jour. Fisheries Res. Bd., Canada, 11: 901-903. [Organism is obligate osmophile, not obligate halophile.]

VALANKOV, A.

1929. Protistenstudien. 4. Die Natur und die systematische Stellung der Labyrinthuleen. Arch. Protistenk., 67: 110-121. [*Labyrinthula zopfii*.]

VESTERGREN, T.

1900. Verzeichnis nebst Diagnosen und Bemerkungen zu meinem Exsiccatenwerke "Micromycetes variores selecti," Fasc. VII-X. Bot. Notiser, 1900: 27-44. [Comments on *Dothidella laminariae* Rostrup and *Pleospora maritima* Rehm.]

VISHNIAC, HELEN S.

1955a. Marine Mycology. Trans. New York Acad. Sci., Ser. 2, 17: 352-360. [Nutritional and culture studies of some marine Phycomycetes and labyrinthulas.]

1955b. The nutritional requirements of isolates of *Labyrinthula* spp. Jour. Gen. Microbiol., 12: 455-463.

1955c. The activity of steroids as growth factors for a *Labyrinthula* sp. Jour. Gen. Microbiol., 12: 464-472.

1955d. The morphology and nutrition of a new species of *Sirolpidium*. Mycologia 47: 633-645. [*S. zoophthorum*. (Cause of disease in clam and oyster larvae.)]

1956. On the ecology of the lower marine fungi. Biol. Bull., 111: 410-414. [Discussion of ecology of molds in marine habitats.]

VISHNIAC, HELEN S. AND S. W. WATSON

1953. The steroid requirements of *Labyrinthula vitellina* var. *pacifica*. Jour. Gen. Microbiol., 8: 248-255.
- WAKSMAN, S. A.
1934. The rôle of bacteria in the cycle of life in the sea. Sci. Monthly, 38: 35-49. [*Aspergillus* and *Penicillium* occur in marine materials.]
- WEHMEYER, L. E.
1948. The developmental pattern within the genus *Pleospora* Rab. Mycologia, 40: 269-294. [Illustrations of ascospores of *P. maritima*.]
- WESTENDORP, G. D.
1859. Sixième notice sur quelques cryptogames inédites ou nouvelles pour la flore belge. Bull. Acad. Royal Belg., II., 7: 77-94. [*Leptosphaeria albopunctata* (described as *Sphaeria albopunctata* n. sp.).]
- WILDEMAN, É. DE
1890. Chytridiacées de Belgique. Ann. Soc. Belge Micro., Mém., 14: 5-28. [*Rhizophydium globosum* on *Melosira*. (Questionable if marine.)]
1893. Notes mycologiques I. Ann. Soc. Belge Micro., Mém., 17: 5-30. [*Rhizophydium marinum*.]
1894. Notes mycologiques III. Ann. Soc. Belge Micro., Mém., 18: 135-161. [Record of *Rhizophydium globosum* on *Melosira*.]
- WILLE, N.
1899. Om nogle Vandsoppe. Vidensk. Selskabs. Skrift., Christiana (Mat.-Nat. Kl.), 1899: 1-14. [*Olpidium dicksonii* var. *striariae*. (Synonymous with *Eurychasma dicksonii*.)]
- WILLIAMSON, H. C.
1913. Report on diseases and abnormalities in fishes: *Dokus adus* an intracapillary parasite of fish. Rept. Fisheries Bd., Scotland, Sci. Investigation, 2: 4-11. [(According to Sproston, 1944, this parasite is identical to *Ichthyosporidium hoferi* in mackerel.)]
- WILSON, IRENE M.
1951. Notes on some marine fungi. Trans. British Myc. Soc., 34: 540-543. [Twenty spp., Pyrenomycetes and Fungi Imperfecti, mentioned, with notes on occurrence.]
1954. *Ceriosporopsis halima* Linder and *Ceriosporopsis cambrensis* sp. nov.: two marine Pyrenomycetes on wood. Trans. British Myc. Soc., 37: 272-285.
1956a. Some marine fungi on wood. Trans. British Myc. Soc., 39: 386. (Abstract)
1956b. Some new marine Pyrenomycetes on wood or rope: *Halophiobolus* and *Lindra*. Trans. British Myc. Soc., 39: 401-415. [*Halophiobolus purpureus* and *H. rufus*, n. spp.; *H. longirostris* new to British Isles; *Lindra inflata* n. gen., n. sp.]
- WINTER, G.
1887. Exotische Pilze IV. Hedwigia, 26:6-18. [*Laestadia prasiolae* n. sp. (Synonymous with *Guignardia prasiolae*, which Hariot, 1887, places in genus *Physalospora*.)]
- WOLF, F. A. AND F. T. WOLF
1947a. The Fungi. Vol. I. Wiley: New York. [Statement on p. 135 to eccrinids on mud crab, *Panopeus herbstii*.]
1947b. The Fungi. Vol. II. Wiley: New York. [Chapter pp. 458-473 on marine fungi; partial bibliography.]

WRIGHT, E. P.

- 1879a. On the cell-structure of *Griffithsia setacea* (Ellis) and the development of its antheridia and tetraspores. Trans. Royal Irish Acad., Dublin, (Sci.), 26: 28-44. [(Portion of descriptive material and figures 4, 5, and 8, pl. 4, are probably of the fungus *Petersenia lobata*.)]
- 1879b. On a species of *Rhizophydium* parasitic on a species of *Ectocarpus*, with notes on the fructification of the Ectocarpi. Trans. Royal Irish Acad., Dublin, (Sci.), 26: 369-379. [*Rhizophydium dicksonii*.]
1881. On *Blodgettia confervoides* of Harvey, forming a new genus and species of fungi. Trans. Royal Irish Acad., Dublin, (Sci.), 28: 21-26. [Harvey's sp. renamed *B. bornetii* n. sp.]

YAMADA, Y.

1934. The marine Chlorophyceae from Ryukyu especially from the vicinity of Nawa. Jour. Fac. Sci. Hokkaido Imp. Univ., (Ser. 5), 2: 33-88. [Association of *Blodgettia* and *Cladophora* reported.]

YOUNG, E. L., III

1937. Notes on the labyrinthulan parasite of the eel-grass *Zostera marina*. Bull. Mt. Desert Island Biol. Lab., pp. 33-35. [Description of organism, which, it is suggested, is *L. macrocystis*; salt tolerance, in culture, reported; results of artificial inoculations. Two new hosts for fungus are reported: *Ruppia maritima* var. *rostrata*, *Zannichellia palustris* var. *major*.]
- 1938a. Recent investigation in the eel-grass problem: preliminary report. Bull. Mt. Desert Island Biol. Lab., pp. 26-28. [Salinity in relation to host, and parasite virulence; suggests temperature and salinity account for sporadic local variations in onset and distribution of disease.]
- 1938b. *Labyrinthula* on Pacific Coast eel-grass. Canad. Jour. Res., 16C: 115-117. [Describes organism as *L. macrocystis*.]
1943. Studies on *Labyrinthula*. The etiologic agent of the wasting disease of eel-grass. Amer. Jour. Bot., 30: 586-593.

ZELLER, S. M.

1918. Fungi found on *Codium mucronatum*. Publ. Puget Sound Marine Sta., 2: 121-125. [*Chytridium*, *Rhizophydium*, *Stemphylium*.]

ZOBELL, C. E.

1946. Marine Microbiology. Chronica Botanica: Waltham, Massachusetts. [Chapter, pp. 129-135, on marine yeasts and molds; historical aspects and partial bibliography.]

ZOBELL, C. E. AND C. B. FELTHAM

1934. Preliminary studies on the distribution and characteristics of marine bacteria. Bull. Scripps Inst. Oceanogr., Tech. Ser., 3: 279-296. [Yeasts from marine materials.]

ZOPF, W.

1887. Ueber einige niedere Algenpilze (Phycomyceten) und eine neue Methode ihre Keime aus den Wasser zu isolieren. Abhandl. Naturforsch. Gesell., Halle, 17: 77-107. [*Rhizophyton sciadii* collected on *Ophiocytium arbusculum* in salt water in culture dishes.]
1888. Zur Kenntnis der Infektions-Krankheiten niedere Thiere und Pflanzen. Nova Acta Acad. Leop.-Carol., 52: 313-376. [*Rhizidium braunii* on diatoms from a salt pool.]

PRELIMINARY ANALYSIS OF THE DISTRIBUTION OF WHITE MARLIN, *MAKAIRA ALBIDA* (POEY), IN THE GULF OF MEXICO¹

ROBERT H. GIBBS, JR.

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts

ABSTRACT

Records of white marlin, *Makaira albida* (Poey), from long-line stations of the Fish and Wildlife Service M/V OREGON indicate a concentration of this species in the Mississippi delta region in midsummer, followed by a gradual dispersal to other parts of the Gulf of Mexico. In April and May the marlin again move northward. The northward distribution and migration appears limited by the 75° surface isotherm. There is no evidence of correlation of either presence or abundance with depth of water. Some distributional similarities between white marlin and yellowfin tuna are noted, and a few pertinent literature references mentioned. The need for further study is emphasized.

INTRODUCTION

The white marlin, *Makaira albida*, is a valued game fish in the western North Atlantic, yet in spite of the avidity of sport fishermen for catching this fish, little is known of its distribution or habits. It is well known that this species apparently congregates in large numbers in the summer off the middle Atlantic states, and that Ocean City, Maryland, has been the principal area from which anglers sought the marlin in this region. Certain areas off southeast Florida, the Bahamas and Cuba appear to harbor white marlin at certain times, but not in the concentration boasted by Ocean City. The fish is sold on the market in Cuba and other West Indian Islands. In the Gulf of Mexico, almost nothing is known.

Beginning in 1954, the U. S. Fish and Wildlife Service vessel OREGON has made a series of cruises, using Japanese long-line gear, to explore the potential production of pelagic fishes, particularly tunas, in the Gulf of Mexico and adjacent waters (Bullis, 1955). Careful records were kept at each station of the entire catch. These records have been kindly made available to me by Harvey R. Bullis. The present analysis is based entirely on these records from the M/V OREGON.

The conclusions or deductions presented here are highly tentative. The study of pelagic fishes is in its infancy; data are difficult to come by and are not usually as complete as would be desired. The major impediment in this study has been the lack of adequate coverage,

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either in time or in area. This is inherent when the accumulation of data is dependent upon an organization, in this case the Fisheries Exploration and Gear Research Section of the U. S. Fish and Wildlife Service, which must be primarily motivated by immediate commercial interests rather than the quest for more abstract scientific information, the value of which is not always readily apparent. Other organizations are presently actively engaged in the study of marlin distribution, particularly the Marine Laboratory of the University of Miami, the American Museum of Natural History, and the Woods Hole Oceanographic Institution. It is hoped that the analysis here will stimulate others to gather similar data in order to fill in gaps and present a more satisfactory picture. Meanwhile, the conclusions which follow may serve as a guide, to stand or fall on the basis of future evidence.

DISTRIBUTION AND MOVEMENTS

The stations at which white marlin were caught by the OREGON are plotted by months in Figure 1. While lack of coverage in vital areas obscures the over-all picture, some conjecture is possible. For all practical purposes, the collections in February and October are too few to contribute anything. Of the others, April and September do not sample the region of the Mississippi Delta (off Louisiana), and July and August do not sample any region except the Delta. In the following discussion, the "Delta region" will refer to the rectangle between about $26^{\circ}30'$ N lat. and the northern Gulf coast, and between 87° and 90° W long.

The weights of the marlin caught were predominantly between 30 and 60 pounds, the range being from 19 to 110 pounds. Using average weights per station, 73 stations fall between 30 and 60 pounds, 2 less than 30, 8 more than 60. The following discussion is therefore based on a rather uniform size group.

Bullis (1955) has noted that yellowfin tuna (*Thunnus albacares*) are apparently absent from the Delta region in March. This seems to be true also for white marlin, as none of four stations produced these fish in that month, which would be most unusual for any other time. In March, however, marlin have been taken in the southwest Gulf and the Bay of Campeche. Beginning in April there is indicated a gradual movement out of the southwest Gulf and toward the Delta region. Despite fairly active collecting in May, no white marlin were taken in the Gulf of Campeche, but each of two stations in the Delta produced them. June stations, despite inadequate coverage, show a



FIGURE 1. Distribution of white marlin in the Gulf of Mexico by months. Black dots = successful stations. Open circles = unsuccessful stations. General range, as indicated by the data, shown by cross-hatched area. 75-degree isotherm from Fuglister, 1947.

decided grouping of marlin at the Delta, with some still slightly westward from it. In July and August, the concentration in the Delta is extremely heavy. As will be shown later, success is the rule in these two months both in number of stations taking marlin and in number

of marlin taken per set. Thus the lack of coverage in other regions does not completely offset the fact that the fish do concentrate in the Delta at this time. This compares to the rather similar concentration off Ocean City, Maryland, also in July and August. Beginning in September, the fish again become dispersed more or less throughout the Gulf.

RELATION TO TEMPERATURE

Some of the above observations may be roughly correlated with temperature distribution. Surface temperatures were recorded at almost all stations. Although the long-line gear usually was fished at 10-20 fathoms, the temperature at the lower depth is probably little different than that at the surface. Even so, the surface temperature may be construed as an index.

On the maps (Figure 1), the approximate contour line for 75° surface temperature is indicated (from Fuglister, 1947). From May through October, the average is nowhere less than 75° in the Gulf, but beginning in November, the 75° contour gradually recedes southward and in March again advances northward. It is noteworthy that almost none of the successful marlin stations have been in water far north of this average 75° contour. The only seemingly anomalous record is one in January in the Delta. Apparently the Delta region has some sort of attraction, generally speaking. Had this anomaly occurred anywhere else, there would have been need for extensive explanation. In the Delta, it is not surprising.

Figure 2 tends to uphold the presumed correlation with the 75° contour. From June through November, all stations were made in water at least 75° at the surface. In the other months, when stations were made in colder water, the lack of success below 74° or 75° is notable. The catch in December at 71° is the anomaly discussed above.

RELATION TO SEASON

In this section, the catch, as judged by number of stations at which at least one marlin was caught and by average number of marlin caught at each station, is analyzed (Table 1).

From April to August in the Delta region, with one exception, half or more of the stations produced marlin. Because of the paucity of stations in April and May, little can be said of these months except that marlin are present. The poor success in June indicates that the concentration is just beginning. In July and particularly in August,

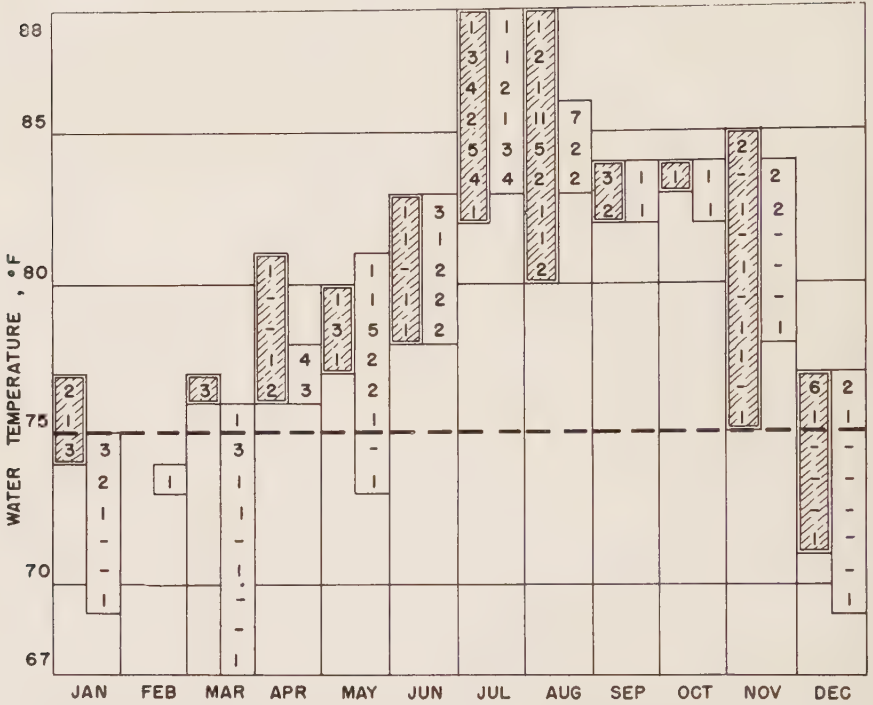


FIGURE 2. Surface temperatures of stations where white marlin were caught (cross-hatched bars) and of unsuccessful stations. Numbers in the bars indicate number of sets at each temperature.

success in both number of stations and average number of fish per station is high. This supports the contention that this is an actual concentration of fish, and is not due merely to the lack of fishing in other areas at the same time. From September through January, the few samples indicate the presence of marlin, but little else. The notable lack of success in February and, especially, March, has already been interpreted as indicating a lack of marlin for a short period, perhaps due to low water temperatures, perhaps to spawning elsewhere.

In areas outside the Delta, few conclusions can be drawn. The average number of fish per successful station is never great. The large number of successful stations in September, all in the northern Gulf, may be sampling fish which are moving away from the Delta, but have not yet dispersed completely. To some extent, success seems dependent upon water temperature, as noted previously. The drop in success in April and May is possibly due to the postulated movement toward the

TABLE 1

Successful and unsuccessful white marlin stations by months.
 S = successful, U = unsuccessful, Avg. fish = average number
 of marlin taken per successful set.

	Non-Delta					Delta				
	S	U	%S	No. Fish	Avg. Fish	S	U	%S	No. Fish	Fish Avg.
Jan.	5	5	50	6	1.2	1	2	33	2	2
Feb.	0	0	—	—	—	0	1	0	—	—
Mar.	3	4	43	7	2.3	0	4	0	—	—
Apr.	3	8	27	4	1.3	1	1	50	2	2
May	3	14	18	4	1.3	2	1	67	2	1
June	2	3	40	3	1.5	2	7	22	2	1
July	0	0	—	—	—	20	12	63	35	1.75
Aug.	0	0	—	—	—	24	11	69	102	4.3
Sept.	5	2	71	8	1.6	0	1	0	—	—
Oct.	0	2	0	—	—	1	0	100	3	3
Nov.	6	5	55	14	2.3	1	0	100	3	3
Dec.	0	1	0	—	—	1	2	33	1	1

Delta and away from the southwest Gulf, where quite a few stations were fished, but where success was poor.

RELATION TO DEPTH OF WATER

Table 2 shows the number of successful stations and the numbers of fish caught in relation to water depths. In the Delta, there are no stations over a bottom deeper than 1,700 fathoms. Here, above bottoms from 500 to 1,200 fathoms, successful stations are the majority. The greatest number of fish per set is over 1,000 fathoms of water. This extremely high average is principally due to three sets made at almost the same point ($28^{\circ} 47-50' N$, $87^{\circ} 48-50' W$) on three consecutive days in August, on which a total of 32 fish were caught. If these are subtracted from the rest, an average catch of 1.8 results, which is actually slightly less than that for the adjacent months.

In the rest of the Gulf, no pattern is shown. Successful stations are scattered over depths of from 600 to 2,100 fathoms. Average catch is consistently somewhat less than at most stations in the Delta. Noteworthy are the catches over depths of more than 1,800 fathoms.

Since white marlin are probably independent of the bottom, these data are useful mainly in further pointing out the wide distribution of the species in the pelagic habitat. The summer congregation, which is over the continental slope, is believed to be a feeding congregation, not

TABLE 2

Successful and unsuccessful white marlin stations according to depth of water. See Table 1 for explanations. Asterisks indicate a station for which number of fish was not recorded.

Depth of Water	Non-Delta					Delta				
	S	U	% S	No. Fish	Avg. Fish	S	U	% S	No. Fish	Avg. Fish
< 100 fm	0	1	0	—	—	0	0	—	—	—
100	0	0	—	—	—	*1	0	100	?	?
200	0	0	—	—	—	0	0	—	—	—
300	0	0	—	—	—	0	1	0	—	—
400	0	1	0	—	—	0	2	0	—	—
500	0	1	0	—	—	3	2	60	10	3.3
600	3	3	50	4	1.3	5	3	63	6	1.2
700	1	2	33	2	2	8	5	62	18	2.25
800	0	2	0	—	—	4	0	100	10	2.25
900	1	1	50	5	5	11	3	79	31	2.8
1000	0	4	0	—	—	8	8	50	41	5.125
1100	2	3	40	3	1.5	4	2	67	9	2.25
1200	3	6	50	7	2.3	2	1	67	8	4
1300	1	3	33	1	1	*3	4	43	5	2.5
1400	0	0	—	—	—	2	4	50	3	1.3
1500	0	2	0	—	—	0	2	0	—	—
1600	1	2	33	1	1	0	2	0	—	—
1700	0	3	0	—	—	0	0	—	—	—
1800	3	2	60	6	2	0	0	—	—	—
1900	3	2	60	5	1.67	0	0	—	—	—
2000	4	3	57	5	1.25	0	0	—	—	—
2100	1	0	100	1	1	0	0	—	—	—
2200	0	1	0	—	—	0	0	—	—	—

a spawning one. Because of nutrients contributed by the Mississippi affluence, this is undoubtedly an area rich in small fish and squids, on which the marlin can feast.

The data also tend to support the reality of this presumed summer congregation in the absence of stations outside the Delta in that season. The number of successful stations is higher, and the average number of fish per station is also high.

Breaking the depth data into months (Table 3) shows no particular correlation of depth with season in regions outside the Delta, and only during the summer in the Delta area.

COMPARISON WITH YELLOWFIN TUNA

Since the primary purpose of the OREGON's long-lining activities was to catch yellowfin tuna, it is of interest to make some rough comparisons between that species and the white marlin. This information has been gleaned from the unpublished cruise reports distributed from

TABLE 3
Successful and unsuccessful white marlin stations by months and by depths. Figures without parentheses = number of marlin. Figures in parentheses = average number of marlin per set. The superscript x indicates that there were unsuccessful stations.

	Non-Delta				Delta			
	Depth Range				Depth Range			
	< 600	600-1099	1100-1599	> 1600	< 600	600-1099	1100-1599	> 1600
Jan.	— ^x	—	1	6(1.5) ^x	—	—	2(2) ^x	—
Feb.	—	—	—	—	— ^x	—	—	—
Mar.	—	—	3(3)	1(1) ^x	—	—	— ^x	—
Apr.	—	1(1) ^x	3(1.5) ^x	— ^x	—	—	2(2)	—
May	— ^x	1(1) ^x	— ^x	2(2) ^x	—	1(1)	1(1)	—
June	—	3(3) ^x	—	—	—	1(1) ^x	— ^x	—
July	—	—	—	—	1(1) ^x	26(1.6) ^x	3(2.7) ^x	—
Aug.	—	—	—	—	14(4.7) ^x	72(4) ^x	8(4)	—
Sept.	—	—	3(1.5) ^x	5(1.7)	—	—	—	—
Oct.	— ^x	—	—	—	—	—	3(3)	—
Nov.	—	7(3.5) ^x	2(2) ^x	4(1.3)	—	3(3)	— ^x	—
Dec.	—	—	—	—	—	—	1(1) ^x	—

Pascagoula, Mississippi. The writer has not gathered complete data on the distribution of yellowfin, but since the stations are the same ones that are plotted on the maps in Figure 1, some deductions may be made.

Table 4 lists the approximate average number of hooks set out for each fish caught by monthly periods. This, roughly, indicates the abundance of the tuna at these times; the smaller the number of hooks,

TABLE 4
Average number of hooks set for each yellowfin tuna caught by month and year. Where open blanks occur, the figure above is a combination for the two months.

	1954	1955	1956	Avg.	Total Sets
Jan.	—	75	258.6	166.8	13
Feb.	—	?	—	?	1
Mar.	—	?	?	?	11
Apr.	?	?	—	?	12
May	126.5	117.2	—	121.9	18
June	—	—	—	—	14
July	19.0	—	35.7	22.4	34
Aug.	56.2	19.8	—	33.0	35
Sept.	46.2	—	—	46.2	8
Oct.	—	—	—	—	3
Nov.	143	—	22.1	33.2	12
Dec.	34.4	—	—	—	13

presumably the more the tuna present. The greatest abundance occurs in July and August, both of which include only the Delta region. In September, there is a slight decline, followed by a strong decline in November. December is anomalously high, but January is again low. No figures are available for February through April, but Bullis' statement (1955) that yellowfins are apparently absent from the Delta in March is significant.

Thus, to a certain extent, the yellowfin show a distributional similarity to white marlin. The catch is rather uniformly low through most of the year, but indicates that they are scattered throughout much of the Gulf. The March disappearance from the Delta suggests that yellowfin, too, may be following a receding isotherm. And again, like the marlin, they apparently concentrate in the Delta during July and August. This concentration, in contrast to presumptions concerning white marlin, is believed to be a spawning phenomenon (Bullis, *in litt.*).

PREVIOUS KNOWLEDGE OF GULF WHITE MARLIN

While white marlin have been well-known from the Atlantic and the West Indies, their presence in the Gulf of Mexico west of the Indies has not been widely noticed. Baughman (1941, 1950) reports sight records from Port Isabel and Port Aransas, Texas, but these appear to be the only references for the area.

The large concentration in the Delta region in July and August, and the similar congregation off Ocean City, Maryland, at the same time, have both been tentatively considered post-spawning feeding congregations. Evidence for this has not been published, but this seems to be the case. Little is known of the spawning habits in the Gulf (or anywhere else for that matter). Few notable concentrations other than the midsummer ones have been noted. Erdman (1956), however, records April as the peak month off Puerto Rico and states that enlarged ovaries have been reported during that month. The best-developed ovary that he had seen was from a fish caught on June 9, 1956. In the sporting literature, Hemingway (in Vesey-Fitzgerald and LaMonte, 1949:156) reports the heaviest run of white marlin north of Cuba in the last two weeks in May. Farrington (*Ibid.* 1:155) notes a "terrific run," the "largest in the Atlantic" in April off Miami Beach, Florida. It is possible that these are spawning runs of some nature, and they do precede the observed summer concen-

trations. The precise nature of these runs, however, needs to be examined, as does that of the summer aggregations.

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OBSERVATIONS ON *ORNITHOTEUTHIS*
ANTILLARUM ADAM, 1957
AN OMMASTREPHID SQUID FROM
THE WEST INDIES¹

GILBERT L. VOSS

The Marine Laboratory, University of Miami

ABSTRACT

Ornithoteuthis volatilis antillarum Adam, 1957 is raised to specific status on the basis of further observed differences from its Japanese relative. The original description is amplified and the radula, spermatophore, funnel organ, suckers, etc. are illustrated. Certain patches within the mantle cavity and on the eyeball are described and considered to be of a light producing nature. The status of the species is discussed.

INTRODUCTION

The present species has only recently been described by W. Adam (1957) who considered it to be a subspecies of the Japanese *Ornithoteuthis volatilis* Sasaki, 1915. Adam's material was obtained from the island of Guadeloupe in the Antilles whereas both of the specimens at hand come from the Bahama Islands. It is presumed that the species is to be found throughout the tropical Western Atlantic.

Adam's paper was received by the author after his own was in galley. However, in view of the added observations, it was decided to rewrite the paper and publish it in order to supplement Adam's excellent description and photographs.

The author wishes to thank Dr. Adam for checking certain points against his own specimens. He also wishes to thank Mr. George Arata, formerly of the Marine Laboratory staff, for the specimens from off Abaco and Mr. Thomas McKenney of the Marine Laboratory for the specimen from the Tongue of the Ocean.

Ornithoteuthis antillarum Adam, 1957

Figs. 1 a-h, 2 a-j

Ornithoteuthis volatilis antillarum Adam, 1957, p. 3, Pl. 1, figs. 1-4.

Geographical distribution. — Bahama Islands; Antilles.

Material studied. 1 male, ML 94.0 mm taken on surface by dipnet off Abaco, Bahamas from U. S. Fish and Wildlife Service R/V THEODORE N. GILL, February, 1952. George Arata, leg. UMML Cat. No. 31.132.

1 female, in alcohol, ML 97.0 mm from southwest edge of the

¹Contribution No. 185 from The Marine Laboratory, University of Miami.

Tongue of the Ocean, Bahamas ($23^{\circ} 27'N$, $77^{\circ} 14'W$) in 5 fathoms of water over sand and rock bottom, dipnet and night light from Marine Laboratory R/V GERDA, July 20, 1957. Thomas McKenney, leg. UMM L Cat. No. 31.94.

Description: The *mantle* is long and slender, its width about 20.0 per cent of the length and widest at the anterior margin, immediately tapering posteriorly to a long, very slender point. The anterior mantle margin is slightly produced dorsally and slightly emarginate beneath the funnel. The *gladius* is not visible through the mantle.

The *fins* are large, their length about one half, their width a little less than half, of the mantle length. The greatest width of the fins is just posterior to the anterior margin which is convex and has a free anterior lobe. The posterior margins are concave, tapering sharply to the attenuate posterior end of the mantle and bordering this is a low ridge which extends to the extremity (Figure 1a).

The *funnel* is strong, deeply set into the funnel groove on the ventral surface of the head and is narrow anteriorly. The funnel groove has a broad foveola anteriorly with about 10-12 longitudinal folds. In both the male and the female there are about 3-4 distinct side pockets on either side of the foveola but the longitudinal folds are not so conspicuous (Figs. 1b and c). The mantle locking apparatus consists of a typical strong ommastrephid type J shaped funnel groove with deep sockets and a similarly shaped ridge on the mantle. The funnel organ has a typically V shaped dorsal member with a small terminal papilla and two fat oval ventral pads (Fig. 1d). The funnel has two strong dorsal bridles.

The *neck* is short with three neck folds on either side, the ventral ones close to the funnel. The neck cartilage is long and slender posteriorly but broad and rounded anteriorly.

The *head* is about as broad as the mantle width and somewhat straight sided. The eyes are large, the eyelids semicircular, truncated posteriorly, rounded anteriorly, with a deep sinus anteriorly which has a downward turn (Fig. 1e). There are both dorsal and ventral windows over the eyes and an examination of the ventral periphery of the eyeball disclosed a long, fairly well defined oval area which seems to be of a luminous nature. In the female this ventral luminous patch is very well defined and distinct (Fig. 1f). Adam informs me that his specimens also have this patch on the eyeball.

The *arms* are long and slender, in the order 2.3.4.1, the first arms

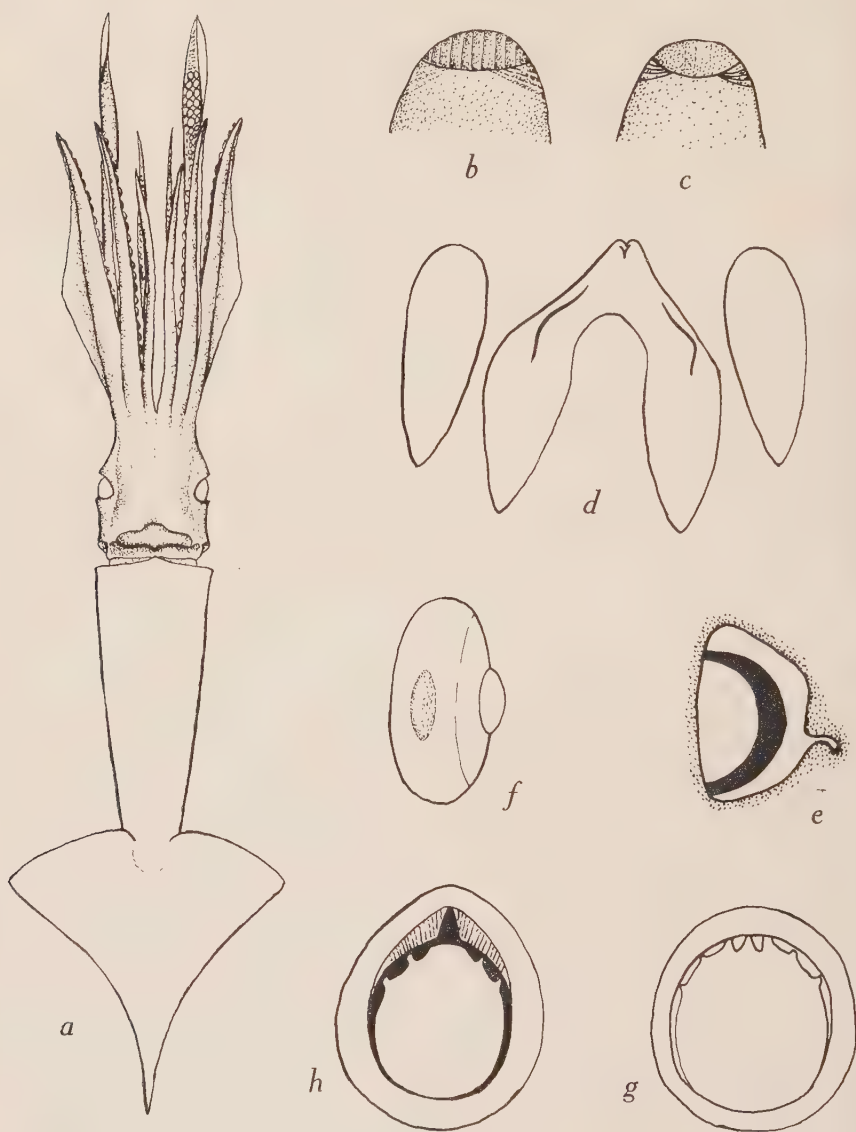


FIGURE 1. *Ornithoteuthis antillarum* Adam, 1957. a. Dorsal view of male, ML 94.0 mm. b. Funnel groove of male. c. Funnel groove of female. d. Funnel organ of male. e. Left eye of female. f. Left eyeball of female to show luminous organ. g. Fourth sucker of ventral row of 2nd arm of male. h. Fourth sucker of dorsal row of 2nd arm of male.

much shorter and more slender than the others. All of the arms are squarish in cross-section. Arm I is rounded dorsally with a low keel on the outer ventral corner. Arm II is rounded as I but also has a rather strong swimming web on the outer ventral corner which extends prominently from the base to the tip of the arm. Arm III has a broad typical swimming membrane on the outer surface which originates at the base of the arm, is deepest about $1/3$ of the distance from the base to the tip, and extends to the extremity. Arm IV is keeled ventrally and has a swimming membrane dorsally. The suckers are in 2 rows, bordered on all of the arms by both dorsal and ventral protective membranes with strong supports, the ventral membranes the deepest on all arms and conspicuous on the third arms where it is deeper than the suckers. The suckers are round, laterally inserted on short pedicels, with the aperture toward the inner median line of the arms.

The dentition of the horny rings of the suckers in the male and the female shows a marked sexual dimorphism, as pointed out by Adam, and to the author's knowledge this must be a rare phenomenon among the oegopsid squids. In the *male* the normal dentition of the suckers on all of the arms is as shown in Figure 2g and h, which are taken from the 3rd left arm. Towards the distal two thirds of the arms there is a tendency towards a slight increase in the number of the long teeth between the large lateral plates. However, on arm II there is a distinct difference in dentition between the suckers of the dorsal and ventral rows for the first 6 pairs. The dentition of the first four dorsal suckers is shown in Figure 1g in which a single large pointed tooth occurs on the inner distal portion of the ring, accompanied by one or two small plate-like teeth on either side. In the first three suckers of the dorsal row the tooth is turned strongly outward. In the fourth it is nearly vertical. In the fifth and sixth it is turned slightly inward and in the seventh on it is of normal appearance. In the first four suckers of the ventral row the horny ring is smooth proximally with two small median teeth accompanied by two small plate-like teeth on either side (Fig. 1h). Beyond the fifth sucker the dentition is of the normal type.

In the *female* the suckers differ consistently from the male in that basally they are composed of about eight plate-like teeth on the distal border but as the middle part of the arm is reached the teeth on the distal border become more numerous and are pointed (Figs. 2e-f). Thus there is not only the normal dentition differences as found on all of the arms but the specialized suckers of the males on the dorso-

lateral pair. What the significance of these modifications is must remain in doubt.

The right ventral arm is *hectocotylized* in the male. Basally there are 9 large suckers similar to those on the other arms. Beyond the 9th sucker they become smaller, have sharper teeth and consist of 8 in the dorsal row and 6 in the ventral row (Figure 2b). Beyond these small suckers they disappear and only a few pedicels remain. The distal third of the arm bears a series of large flattened, triangular pedicels folded over onto the ventral border which extend to the distal part of the arm. On the midsection of the ventral side of the arm, occupying about $\frac{1}{4}$ of the length, is a peculiar honeycomb-like structure shown in Figure 2c.

The *tentacles* are fairly short, strongly compressed and sharply keeled for their entire length on the aboral surface, the keel expanded to a swimming web on the aboral surface of the club. The oral surface is flattened and grooved medially. The expanded club occupies about $\frac{1}{3}$ of the length of the tentacle, the sucker bearing part of the arm being about $\frac{1}{2}$ of the tentacle length. The entire sucker bearing portion is bordered by a strong protective membrane on either side and has strong supports. There are about 6 pairs of small suckers on the stalk, gradually increasing in size to the club. The suckers of the hand are in 4 rows, the two inner rows bearing suckers which are large, round and with wide apertures, the horny ring bearing about 18-20 sharp, round, curved teeth which are widely separated (Figure 2i). The dorsal and ventral marginal rows bear small suckers which have about 10-12 small sharp teeth on the outer border only, the inner half being entire. The large hand suckers consist of about 6 pairs after which the suckers abruptly decrease in size and continue in 4 rows to the tip of the club. The distal suckers are largest in the ventral row and decrease in size dorsally. They are toothed on their entire margin, the teeth, about 8 in number, being long and sharp on the outer margin and small, blunt and plate-like on the remaining part of the margin. Distally there is a small round cluster of about 18 suckers with smooth rings (Fig. 2d).

The *buccal membrane* has seven lappets and seven supports.

The mantle was laid open ventrally and a *luminous organ* was found on the ventral surface of the viscera. It consists of a round pinkish patch on the ventral surface at the anterior end of the liver just below the funnel and 4.0 mm in diameter. Running posteriorly from this along the midline is a thin threadlike pink streak which after about

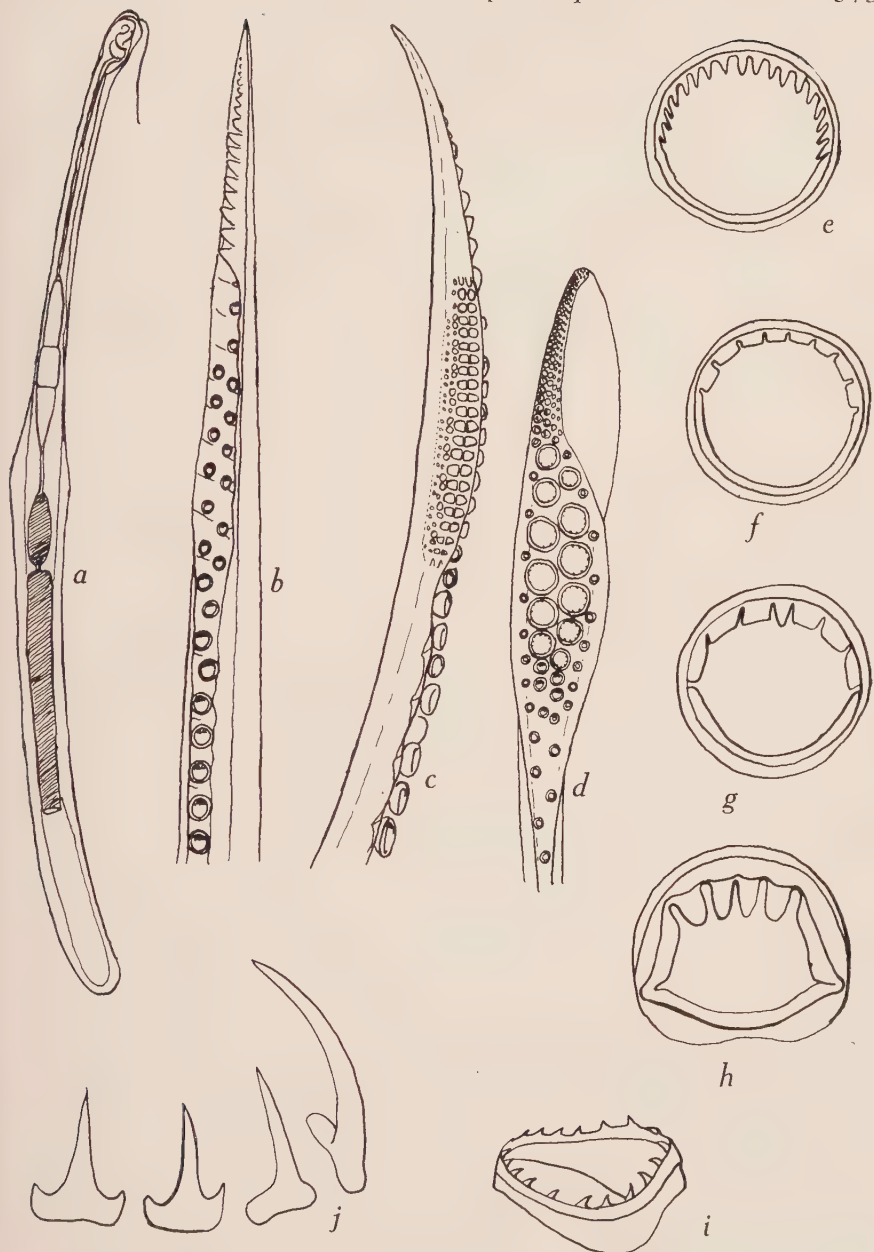


FIGURE 2. *Ornithoteuthis antillarum* Adam, 1957. a. Spermatophore, 6.0 mm total length. b. Oral view of hectocotylyzed right arm of male. c. Side view of hectocotylyzed right arm of male. d. Oral view of right tentacular club of male. e. Tenth sucker of 3rd arm of female. f. Fifth sucker of 3rd arm of female. g. Sixth sucker of 3rd arm of male. h. Twelfth sucker of 3rd arm of male. i. Large tentacular sucker of male. j. Radula of male.

10.0 mm widens out to a broad streak nearly 2.0 mm wide. This gradually tapers down posteriorly and extends to the tip of the mantle. Just below the level of the branchial hearts there is a narrow oval split in the streak to permit the passage of the pallial artery. In the female the anterior end of the luminous organ is oval and more nearly compares to Sasaki's figure of *O. volatilis* both in shape and location.

Dr. Adam informed me that on reexamination of his specimens he found a second organ (luminous?) just before the anal opening and on the ventral side of the rectum. Examination of the specimens before me discloses what may be such an organ but it is not easily differentiated.

TABLE 1

Measurements (in mm) and proportions of two specimens of *Ornithoteuthis antillarum*, from the Bahama Islands

Sex	Male	Female
ML	94.0	97.0
MWI	20.2	20.1
HLI	23.9	20.6
HWI	20.2	23.2
FLI	52.1	53.6
FWI	47.9	48.5
Arms		
I	41.0	33.0
II	49.0	43.0
III	51.0	43.0
IV	46.0	37.5
TLI	84.0	80.5
CLI	30.8	27.3
ALI	54.3	44.3

The penis of the male contained several *spermatophores* and one of these is shown in Figure 2a. The spermatophore was 6.0 mm in length and 0.3 mm in greatest diameter. A noticeable feature of all of those examined was the swelling of the outer wall in the mid region.

The *radula* was extracted from the female and is shown in Figure 2j.

The stomach of the male was opened for examination of its contents. A large amount of remains were examined and found to be mostly from an *Abralia* of about 30.0 mm ML, probably *A. varanyi*. Besides these remains there were parts of a caridean shrimp and a few fish scales.

The male specimen has apparently lost the epidermis containing the chromatophores and in preservation is a uniform yellowish color.

The female from the Tongue of the Ocean has the skin intact. Dorsally and less so ventrally the body is brownish purple, densely so dorsally, but lighter on the tail where are found mostly scattered large purple spots and smaller brownish ones. Ventrally and laterally there is a considerable silvery sheen which is also apparent on the sides of the head. The dorsal arms are brownish purple, the lateral arms speckled with small pigment spots and a silvery wash.

Mr. McKenney, in describing the colors of the female from off Andros, reports that while the chromatophores changed rapidly, thus turning the skin dark, or transparent, there seemed to emanate an opal color which he thinks may have originated from the light organs in the mantle cavity.

Discussion. Adam (1957, p. 7) has carefully compared this species with *O. volatilis* from Japan. From this latter species it differs in (1), the structure of the hectocotylus, (2), the dimorphism of the dentition of the sessile suckers and the specialized suckers of the male, (3), the presence of a luminous organ on the ventral periphery of the eyeball mostly from an *Abralia* of about 30.0 mm ML, probably *A. veranyi*, and the (4) possible presence of another light organ on the ventral surface of the rectum. These last two were not noted by Adam in his paper and are not mentioned by Sasaki in his description of *O. volatilis*. Because of these differences the present author believes that these specimens represent a distinct species rather than a subspecies as Adam suggested. Of course, until a direct comparison can be made with representatives of the Japanese species this must at best remain uncertain, but it does not seem likely that Sasaki would have overlooked such important details.

The structure of the funnel groove also bears examination. Sasaki reports that there are no folds or side pockets in the Japanese form. Adam also did not find them in his specimens from Guadeloupe. However, folds are prominent in the male from Abaco but indistinct in the female. It is possible that the side pockets which are plainly seen in the female but are more difficult to find in the male are not of the same nature as those found in some of the other ommastrephids and the variableness of their occurrence casts doubt upon their value as systematic characters in this species.

Mr. McKenney, who observed this species alive around the light, commented upon their great agility. Sasaki states that the Japanese species often darts out of the water "flying" above the surface which probably accounts for Okada's (1927) generic name, *Ornithoteuthis*,

or bird squid. Sasaki preferred to keep his species in the genus *Ommastrephes* but I agree with Adam that the differences enumerated above and in his paper are sufficient to validate the use of *Ornithoteuthis* for the two species.

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